

ENDANGERED SPECIES ACT STATUS REVIEW REPORT:

Giant Manta Ray (*Manta birostris*)



Photo Credit: NOAA; Flower Garden Banks

Reef Manta Ray (*Manta alfredi*)



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DISCLAIMER

This document does not represent a decision by the National Marine Fisheries Service (NMFS) on whether these species should be proposed for listing as threatened or endangered under the Endangered Species Act of 1973 (ESA).

EXECUTIVE SUMMARY

This report was produced in response to a petition received from Defenders of Wildlife on November 10, 2015, to list the giant manta ray (*Manta birostris*) and reef manta ray (*M. alfredi*) as endangered or threatened under the Endangered Species Act (ESA). On February 23, 2016, the National Marine Fisheries Service (NMFS) announced in the *Federal Register* that the petition had sufficient merit for consideration and that a status review was warranted for these two species (81 FR 8874). This report is the status review for the giant and reef manta ray. This report summarizes the best available data and information on the two species and presents an evaluation of each species' status and extinction risk.

Manta birostris, the giant manta ray, is found worldwide in tropical, subtropical, and temperate bodies of water. It is commonly found offshore, in oceanic waters, and near productive coastlines. The giant manta ray is considered to be a migratory species, with estimated distances travelled of up to 1,500 km. Yet, despite their large range, the species is infrequently encountered (with the exception of a few areas noted for manta ray aggregations). There are no current or historical estimates of the global abundance of *M. birostris*, with most estimates of subpopulations based on anecdotal diver or fisherman observations, which are subject to bias. These populations potentially range from around 100-1,500 individuals.

The most significant threat to the giant manta ray is overutilization for commercial purposes. Giant manta rays are both targeted and caught as bycatch in a number of global fisheries throughout their range, and are most susceptible to industrial purse-seine and artisanal gillnet fisheries. With the expansion of the international mobulid gill raker market and increasing demand for manta ray products, estimated take of giant manta rays, particularly in many portions of the Indo-Pacific, frequently exceeds numbers of identified individuals in those areas. Observations from these areas also indicate declines in sightings and landings of the species. Efforts to address overutilization of the species through regulatory measures appear inadequate, with evidence of targeted fishing of the species despite prohibitions and only one regional measure to address bycatch issues, with uncertain effectiveness.

Given the species' extremely low reproductive output and overall productivity, it is inherently vulnerable to threats that would deplete its abundance, with a low likelihood of recovery. Although there is considerable uncertainty regarding the species' current abundance throughout its range, the best available information indicates that the species has experienced population declines of potentially significant magnitude due to fisheries-related mortality within the Indo-Pacific and eastern Pacific portion of its range, which we determined qualifies as a "significant portion its range" under the final Significant Portion of Its Range (SPR) policy (79 FR 37577; July 1, 2014). And while larger subpopulations of the species still exist in this SPR, including off Mozambique, Ecuador, and potentially Thailand, giant manta rays are a migratory species and will continue to face fishing pressure and experience fisheries-related mortality particularly in the industrial purse-seine fisheries and artisanal gillnet fisheries operating throughout the SPR. Therefore, we conclude that overutilization will continue to be a threat to these remaining *M. birostris* populations through the foreseeable future, placing the species at a moderate risk of extinction throughout a significant portion of its range.

Manta alfredi, the reef manta ray, is only observed in the Indian Ocean and the western and south Pacific. Prior to 2009, all manta species were identified as *M. birostris*, and, as such, information on the historical range, abundance and distribution of the species is scarce. *Manta alfredi* is commonly seen along productive nearshore environments (such as island groups, shallow reefs, or near upwelling events), and appears to avoid colder waters (< 21°C). Reef manta rays are considered a more resident species than giant manta rays (with residencies estimated at up to 1.5 years) and exhibit a degree of site-fidelity, returning to known aggregation areas. However, current global population numbers are unknown and no historical baseline data exist. Local populations of *M. alfredi* have not been well assessed either, but appear to be generally small, sparsely distributed, and isolated. Photo-identification studies suggest subpopulations may range from 100 to 350 individuals, with some areas home to larger populations of up to 802 to 9,677 individuals.

Given their more inshore distribution and association with shallow coral and rocky reefs, *M. alfredi* does not appear to be as vulnerable to commercial and larger-scale artisanal fishing operations as *M. birostris*. In fact, many of the identified populations of *M. alfredi* are currently protected by fishing regulations and appear stable, indicating that these existing regulatory measures are adequate at protecting the species from declines due to fishing mortality. In terms of other threats, climate change was identified as potentially contributing to the long-term extinction risk of the species, given the association of *M. alfredi* with coral reefs. However, although coral reef community structure and zooplankton abundance and distribution are likely to be altered as a result of climate change through the foreseeable future; what this change will look like and its subsequent impact on the species is highly uncertain.

Overall, despite the inherent demographic risks that the species faces (e.g., small, isolated populations, low productivity), the species does not appear to be subject to significant threats that are causing declines, or likely to cause declines, to the point where the species would be at risk of extinction. While climate change may alter aspects of the habitat and food resources of the species, the subsequent impact on the species is highly uncertain. Furthermore, no significant portions of the species' range could be identified. Thus, based on the evaluation of demographic risks and threats to the species, we conclude that the reef manta ray is likely to be at a low overall risk of extinction throughout its range.

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INTRODUCTION

Scope and Intent of the Present Document

This document is the status review in response to a petition¹ to list giant and reef manta rays under the Endangered Species Act (ESA). Under the ESA, if a petition is found to present substantial scientific or commercial information that the petitioned action may be warranted, a status review shall be promptly commenced (16 U.S.C. 1533(b)(3)(A)). The National Marine Fisheries Service (NMFS) determined that the petition had sufficient merit for consideration and that a status review was warranted (81 FR 8874, February 23, 2016).

This document is the scientific review of the biology, population status and future outlook for the two manta ray species. It provides a summary of the available data and information on both species, and presents evaluations of each species' status and extinction risk. The conclusions in this status review are subject to revision should important new information arise in the future. Where available, there are literature citations to review articles that provide even more extensive citations for each topic. Public comments, data and information were reviewed through December 2016.

LIFE HISTORY AND ECOLOGY

Taxonomy and Distinctive Characteristics

Scientific Classification	
Kingdom	Animalia
Phylum	Chordata
Class	Chondrichthyes
Subclass	Elasmobranchii
Superorder	Batoidea
Order	Myliobatiformes

¹ (1) Defenders of Wildlife to U.S. Secretary of Commerce, acting through the National Oceanic and Atmospheric Administration and the National Marine Fisheries Service, November 10, 2015, "A petition to list the giant manta ray (*Manta birostris*), reef manta ray (*Manta alfredi*), and Caribbean manta ray (*Manta c.f. birostris*) as endangered, or alternatively as threatened, species pursuant to the Endangered Species Act and for the concurrent designation of critical habitat."

Scientific Classification		
Family	Myliobatidae	
Subfamily	Mobulidae	
Genus	<i>Manta</i> (Bancroft, 1829)	
Species	<i>birostris</i> (Walbaum, 1792)	<i>alfredi</i> (Kreffft, 1868)
Common	Oceanic Manta Ray, Giant Manta Ray, Pacific Manta Ray, Pelagic Manta Ray	Reef Manta Ray, Coastal Manta Ray, Inshore Manta Ray, Prince Alfred's Ray, Resident Manta Ray

The manta ray was first described by Walbaum in 1792. These large bodied, planktivorous rays are considered part of the Mobulidae, a subfamily that appears to have diverged from Rhinoptera around 30 million years ago (Poortvliet et al. 2015). *Manta* species are distinguished from other *Mobula* in that they tend to be larger, with a terminal mouth, and have long cephalic fins (Evgeny 2010). The genus *Manta* has a long and convoluted taxonomic history due partially to the difficulty of preserving such large specimens and conflicting historical reports of taxonomic characteristics (Couturier et al. 2012; Kitchen-Wheeler 2013). All manta rays were historically categorized as *Manta birostris*, but Marshall et al. (2009) presented new data that supports the splitting of the monospecific *Manta* genus into two species: *M. birostris* and *M. alfredi* (Figure 1).

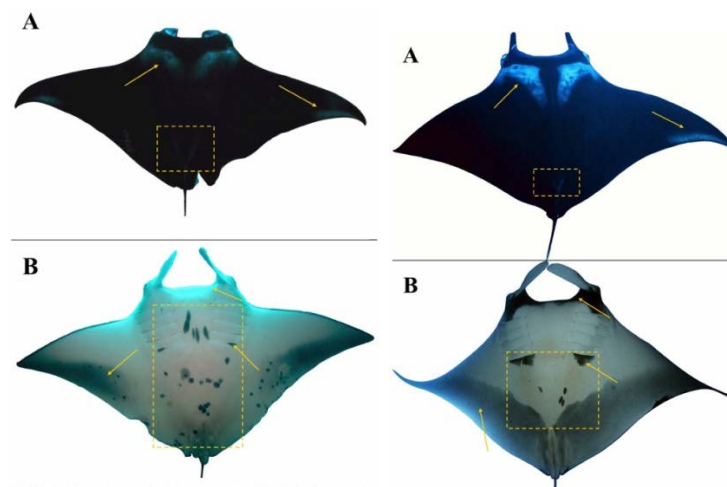


Figure 1. General characteristics and natural coloration patterns in *Manta alfredi* (left) and *Manta birostris* (right) (A) dorsal surface, arrows pointing to the shape and coloration of the shoulder patches and the coloration on the pectoral fins, box showing chevron shaped marking anterior to dorsal fin. (B) ventral surface, box showing region of highest spot density and distribution, arrows showing size of spot anterior to the 5th gill slit, coloration of mouth region, and coloration of the pectoral fin margin. Source: Marshall et al. (2009).

Both *Manta* species have diamond-shaped bodies with wing-like pectoral fins; the distance over this wingspan is termed disc width (DW). There are two distinct color types in both species: chevron and black (melanistic). Most of the chevron variants have a black dorsal surface and a white ventral surface with distinct patterns on the underside that can be used to identify individuals (Marshall et al. 2008; Kitchen-Wheeler 2010; Deakos et al. 2011). While these markings are assumed to be permanent, there is some evidence that the pigmentation pattern of *M. birostris* may actually change over the course of development (based on observation of two individuals in captivity), and thus caution may be warranted when using color markings for identification purposes in the wild (Ari 2015). The black color variants of both species are entirely black on the dorsal side and almost completely black on the ventral side, except for areas between the gill-slits and the abdominal area below the gill-slits (Kitchen-Wheeler 2013).

Marshall et al. (2009) provided a key to distinguishing between the two species based on physical characters such as coloration, dentition, denticles, spine morphology, size at maturity, and maximum DW. Only *M. birostris* has a caudal thorn (Marshall et al. 2009). *M. birostris* is also larger than *M. alfredi*, having been documented to grow as large as 6.8 meters DW (Kunjipalu and Boopendranath 1982). In contrast, *M. alfredi* on average grows to a DW of 4 meters (Marshall et al. 2011b). Additionally, the skin of *M. birostris* forms prominent dermal denticles with pronounced bifid cusps randomly distributed along sagittally oriented ridges in the skin on both the ventral and dorsal surfaces, giving their skin a much rougher appearance than that of *M. alfredi* (Marshall et al. 2009).

In terms of coloration, the chevron variant of *M. birostris* can be distinguished from the chevron *M. alfredi* color type by its large, white, triangular shoulder patches that run down the middle of its dorsal surface, in a straight line parallel to the edge of the upper jaw (Marshall et al. 2009). The species also has dark (black to charcoal grey) mouth coloration, medium to large black spots that occur below its fifth gill slits, and a grey V-shaped colored margin along the posterior edges of its pectoral fins (Marshall et al. 2009). In contrast, the chevron *M. alfredi* has pale to white shoulder patches where the anterior margin spreads posteriorly from the spiracle before curving medially, a white to light grey mouth, dark spots that are typically located in the middle of the abdomen, in between the five gill slits,

and dark colored bands on the posterior edges of the pectoral fins that only stretch mid-way down to the fin tip (Marshall et al. 2009).

The melanistic form of both species, as mentioned before, are entirely black dorsally and black on the ventral side as well with the exception of areas around the gill-slits and posterior to the gill-slits. Spot patterns similar to those seen in the respective chevron types are usually visible along the white abdominal region in the mid-line area, with spot patterning absent between the gill-slits for *M. birostris* but present for *M. alfredi* (Marshall et al. 2009). A leucistic color form (mostly white) has also been documented for both species, but appears to be rare (Marshall et al. 2009).

Recently, a taxonomic study suggested that these two manta ray species may actually be closely related to the Chilean devil ray (*Mobula tarapacana*), with genetic analyses that support nesting these species under the genus of *Mobula* rather than *Manta* (White et al. 2017). However, until formally accepted by the scientific community, we recognize *Manta alfredi* and *Manta birostris* as two species under the genus *Manta*.

Historical Range, Distribution and Habitat Use

Manta species are circumglobal in range, but within this broad distribution, individual populations are scattered and highly fragmented (CITES 2013). The ranges of the two Manta species sometimes overlap; however, at a finer spatial scale, the two species generally appear to be allopatric within those habitat areas (Kashiwagi et al. 2011) and exhibit different habitat use and movement patterns (inshore versus offshore reef habitat use) (Marshall and Bennett 2010b; Kashiwagi et al. 2011). Clark (2010) suggests that the larger *M. birostris* may forage in less productive pelagic waters and conduct seasonal migrations following prey abundance whereas *M. alfredi* is more of a resident species in areas with regular coastal productivity and predictable prey abundance. Kashiwagi et al. (2010) observed that even in areas where both species are found in large numbers at the same feeding and cleaning sites, the two species do not interact with each other (e.g., they are not part of the same feeding group and males of one species do not attempt to mate with females of the other species). Additional studies on habitat use for both species are needed, particularly investigating how these individuals influence their environment, as

studies have shown that the removal of large plankton feeders, like manta rays, from the ecosystem can cause significant changes in species composition (Springer et al. 2003).

***M. birostris* (Giant Manta Ray)**

In terms of range, within the Northern hemisphere, the species has been documented as far north as southern California and New Jersey on the United States west and east coasts, respectively, and Mutsu Bay, Aomori, Japan, the Sinai Peninsula and Arabian Sea, Egypt, and the Azores Islands (Gudger 1922; Kashiwagi et al. 2010; Moore 2012; CITES 2013). In the Southern Hemisphere, the species occurs as far south as Peru, Uruguay, South Africa, New Zealand and French Polynesia (Mourier 2012; CITES 2013). In 2015, Couturier et al. (2015) documented the presence of the species for the first time in waters off eastern Australia, with two individuals photographed off Montague Island in New South Wales and off the northeast coast of Tasmania, extending the known range of the species to 40°S. De Boer et al. (2015) recently confirmed the presence of *M. birostris* in offshore shallow waters of Suriname, in depths between 28 and 42 m; however, local fishermen were familiar with the species, indicating that it likely occurs regularly in these waters. While historical reports of distribution do not take into account the recent splitting of the genus (Marshall et al. 2009), there is no information to suggest a change in the historical range of *M. birostris*.

Lawson et al. (2016) recently developed a map that shows the Extent of Occurrence (EOO) and Area of Occupancy (AOO) of *M. birostris* based on current knowledge of the species' distribution. The EOO was defined as: "the area contained within the shortest continuous imaginary boundary which can be drawn to encompass all the known, inferred or projected sites of present occurrence of a taxon" and the AOO was defined as "the area within its 'extent of occurrence' that is occupied by a taxon for each country. The AOO measure reflects the fact that a taxon will not usually occur throughout the area of its extent of occurrence, which may, for example, contain unsuitable habitats or be beyond the maximum depth distribution." Only areas where the presence of the species has been confirmed were included in the AOO. **Figure 2** provides the depiction of the AOO and EOO of the giant manta ray.

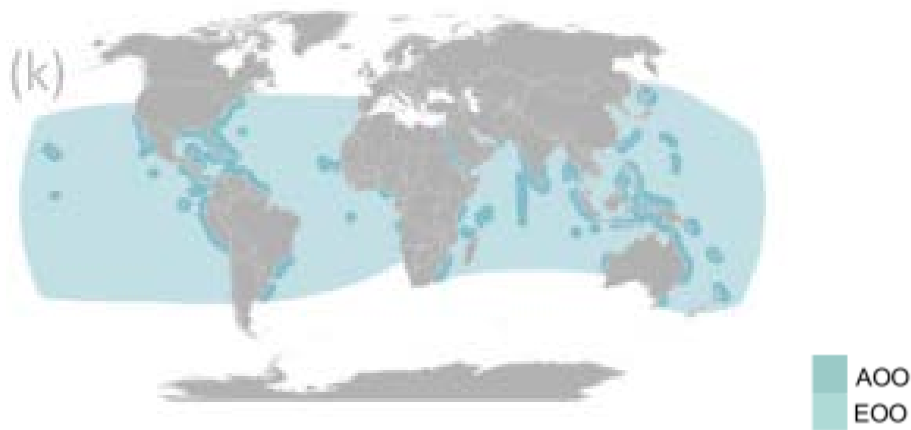


Figure 2. Map depicting the Extent of Occurrence (EEO) and Area of Occupancy (AOO) of *Manta birostris* based on current knowledge of the species' distribution. Source: Lawson et al. (2016)

Despite this large range, sightings are often sporadic with the exceptions of the Similan Islands (Thailand), Raja Ampat (Indonesia), northeast North Island (New Zealand), Kona, Hawaii (USA), Laje de Santos Marine Park (Brazil), Isla de la Plata (Ecuador), Ogasawara Islands (Japan), Isla Margarita and Puerto la Cruz (Venezuela), northern cost of the Yucatan Peninsula, Isla Holbox, Revillagigedo Islands, and Bahia de Banderas (Mexico), where more regular sightings are common (Notarbartolo-di-Sciara and Hillyer 1989; Homma et al. 1999; Duffy and Abbott 2003; Luiz et al. 2009; Clark 2010; Kashiwagi et al. 2010; Marshall et al. 2011a; Stewart et al. 2016a; Hacothen-Domené et al. 2017). The timing of these sightings varies by region (for example, the majority of sightings in Brazil occur during June and September, while in New Zealand sightings mostly occur between January and March) and seems to correspond with the movement of zooplankton, current circulation and tidal patterns, seasonal upwelling, seawater temperature, and possibly mating behavior (Couturier et al. 2012; De Boer et al. 2015; Armstrong et al. 2016; Hacothen-Domené et al. 2017). For example, off the coast of South America, De Boer et al. (2015) suggest that the presence of *M. birostris* likely coincides with the rainy season and subsequent outflows of nutrient-rich water and low salinity front from associated river systems. Off the northern Yucatan peninsula, Hacothen-Domené et al. (2017) found that higher probability of *M. birostris* occurrence was also seasonal and associated with sea surface temperatures $>27^{\circ}\text{C}$,

higher primary productivity ($4,500 \text{ mg C}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$), shallow waters ($<10 \text{ m}$), distance to shore ($<50 \text{ km}$), and bottom slope ($<0.5^\circ$)

Within its range, *M. birostris* inhabits tropical, subtropical, and temperate bodies of water and is commonly found offshore, in oceanic waters, and near productive coastlines (Figure 2) (Marshall et al. 2009; Kashiwagi et al. 2011). As such, giant manta rays can be found in cooler water, as low as 19°C , although temperature preference appears to vary by region, with *M. birostris* off the U.S. east coast commonly found in waters from 19 - 22°C and those off the Yucatan peninsula and Indonesia between 25 - 30°C (Duffy and Abbott 2003; Marshall et al. 2009; Freedman and Roy 2012; Graham et al. 2012; Hacothen-Domené et al. 2017). The species has also been observed in estuarine waters near oceanic inlets, with use of these waters as potential nursery grounds (Adams and Amesbury 1998; Milessi and Oddone 2003; Medeiros et al. 2015).

Although giant manta rays are considered more oceanic and solitary than *M. alfredi*, they have been observed congregating at cleaning sites at offshore reefs and feeding in shallow waters during the day at depths $<10 \text{ m}$ (O'Shea et al. 2010; Marshall et al. 2011a; Rohner et al. 2013). In fact, giant manta rays appear to exhibit a high degree of plasticity in terms of their use of depths within their habitat. Tagging studies have shown that the species conducts night descents to 200 - 450 m depths (Rubin et al. 2008; Stewart et al. 2016b) but is capable of diving to depths exceeding $1,000 \text{ m}$ (A. Marshall et al. unpubl. data 2011 cited in Marshall et al. (2011a)). The species has a rete mirabile cranica as a counter-current heat exchanger around the brain that possibly facilitates its use of these cooler habitats (Alexander 1996). Stewart et al. (2016b) found diving behavior may be influenced by season, and more specifically, shifts in prey location associated with the thermocline, with tagged giant manta rays ($n=4$) observed spending a greater proportion of time at the surface from April to June and in deeper waters from August to September.

The giant manta ray is considered to be a migratory species, with satellite tracking studies using pop-up satellite archival tags registering movements of the giant manta ray from Mozambique to South Africa (a distance of $1,100 \text{ km}$), from Ecuador to Peru (190 km), and from the Yucatan, Mexico into the Gulf of Mexico (448 km) (Marshall et al. 2011a). In a

tracking study of six *M. birostris* individuals from off Mexico's Yucatan peninsula, Graham et al. (2012) calculated a maximum distance travelled of 1,151 km (based on cumulative straight line distance between locations; tag period ranged from 2 to 64 days). Similarly, Hearn et al. (2014) report on a tagged *M. birostris* that was tracked from Isla de la Plata (Ecuador) to west of Darwin Island (tag was released after 104 days), a straight-line distance of 1,500 km, further confirming that the species is capable of fairly long distance migrations but also demonstrating connectivity between mainland and offshore islands. However, a recent study by Stewart et al. (2016a) suggests that the species may not be as highly migratory as previously thought. Using pop-up satellite archival tags in combination with analyses of stable isotope and genetic data, the authors found evidence that *M. birostris* may actually exist as well-structured subpopulations that exhibit a high degree of residency. For example, unlike the giant manta ray in the Hearn et al. (2014) study, tagged *M. birostris* individuals from locations nearshore to Mexico (Bahia de Banderas ; n=5) and offshore Mexico (Revillagigedo Islands; n=4) showed no movements between locations (tag deployment length ranged from 7 days to 193 days) (Stewart et al. 2016a). The stable isotope analysis showed higher $\delta^{13}\text{C}$ values for the nearshore mantas compared to those offshore, indicating these mantas were foraging in their respective locations rather than moving between nearshore and offshore environments (Stewart et al. 2016a). Additionally, using double digest restriction-site associated DNA sequencing from DNA extracted from white muscle tissue of mantas, the authors found evidence of population structure between the coastal Mexico and offshore Mexico populations (Stewart et al. 2016a). While the authors note that the species may be capable of occasional long-distance movements, the results from the study indicate that these movements may be rare and may not contribute to substantial gene flow or interpopulation mixing of individuals (Stewart et al. 2016a).

***M. alfredi* (Reef Manta Ray)**

Manta alfredi is only observed in the Indian Ocean and the western and south Pacific (Figure 3). The northern range limit for the species in the western Pacific is presently known to be off Kochi, Japan (32°48'N, 132°58'E) and its eastern limit in the Pacific is known to be Fatu Hiva in French Polynesia (10°29'S; 138°37'W) (Kashiwagi et al. 2010; Mourier 2012). *M. alfredi* is known to aggregate in waters off Australia (McGregor et al.

2008; Jaime et al. 2014), Hawaii (Clark 2010; Deakos et al. 2011), Japan (Ishihara and Homma 1995; Homma et al. 1999; Yano et al. 1999b), Tahiti (De Rosemont 2008), Mozambique (Marshall et al. 2008; Marshall et al. 2009), the Maldives (Kitchen-Wheeler 2010), and the Marquesas Islands (Mourier 2012). Lawson et al. (2016) provide a map that shows the EOO and AOO of *M. alfredi* based on current knowledge of the species' range and distribution. Only areas where the presence of the species had been confirmed were included in the AOO (however, note that this map does not take into account the recent observation of the species off Kochi, Japan). **Figure 3** provides the depiction of the AOO and EOO of the reef manta ray.

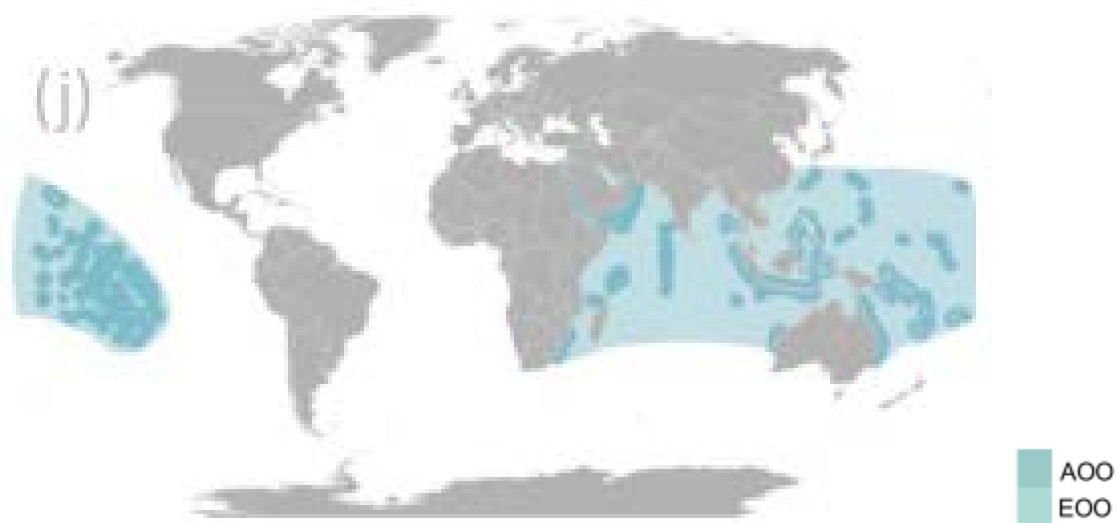


Figure 3. Map depicting the Extent of Occurrence (EOO) and Area of Occupancy (AOO) of *Manta alfredi* based on current knowledge of the species' distribution. Source: Lawson et al. (2016)

It is difficult to estimate the historical range of *M. alfredi* due to confusion until recently about its identification (Marshall et al. 2009). For example, prior to the splitting of the genus, it was assumed that all manta rays found in the Philippines were *M. birostris*; however, based on recent survey efforts, it has been confirmed that both *M. birostris* and *M. alfredi* occur in these waters (Verdote and Ponzo 2014; Aquino et al. 2015; Rambahiniarison et al. 2016). This may be the case elsewhere through its range and underscores the need for concentrated survey effort in order to better understand the distribution of these two manta ray species.

M. alfredi is commonly seen inshore near coral and rocky reefs and appears to avoid colder waters (< 21°C) (Rohner et al. 2013; Braun et al. 2014). Reef manta rays prefer habitats along productive nearshore environments (such as island groups or near upwelling events) and are considered a more resident species than *M. birostris* (Homma et al. 1999; Dewar et al. 2008; Clark 2010; Kitchen-Wheeler 2010; Anderson et al. 2011a; Deakos et al. 2011; Marshall et al. 2011b; McCauley et al. 2014), with residencies estimated at up to 1.5 years (Clark 2010). However, recent tracking studies, while showing evidence of site fidelity (Clark 2010; Couturier et al. 2011; Deakos et al. 2011), also indicate that *M. alfredi* is capable of traveling long distances (e.g., >700 km), similar to *M. birostris*. For example, Jaine et al. (2014) tagged 10 reef manta rays and tracked them over the course of 736 days. Average track length was 1,169 km (\pm 640 SD) with one manta ray traveling 2,441 km in 118 days (Jaine et al. 2014). Dispersal distances from the tagging site were as far as 520 km, indicating that this species can undertake long-distance movements and utilize deep, offshore environments to exploit productive hotspots (which, in this case, was the Capricorn Eddy region; see **Figure 4**). Similarly, using photo-identification of reef manta rays in south-central Indonesia, Germanov and Marshall (2014) found that *M. alfredi* are capable of rapid, long-distance movements (up to 450 km straight-line distance), with migration routes throughout the Indonesian Archipelago. These routes suggest potential connectivity of reef manta rays between neighboring islands and indicate that the species could be capable of international migrations in some portions of their range. Connectivity between islands in Japan has also been observed, with Yano et al. (1999a) remarking on the migration of manta rays between the Yaeyama Islands and the Miyako Islands.

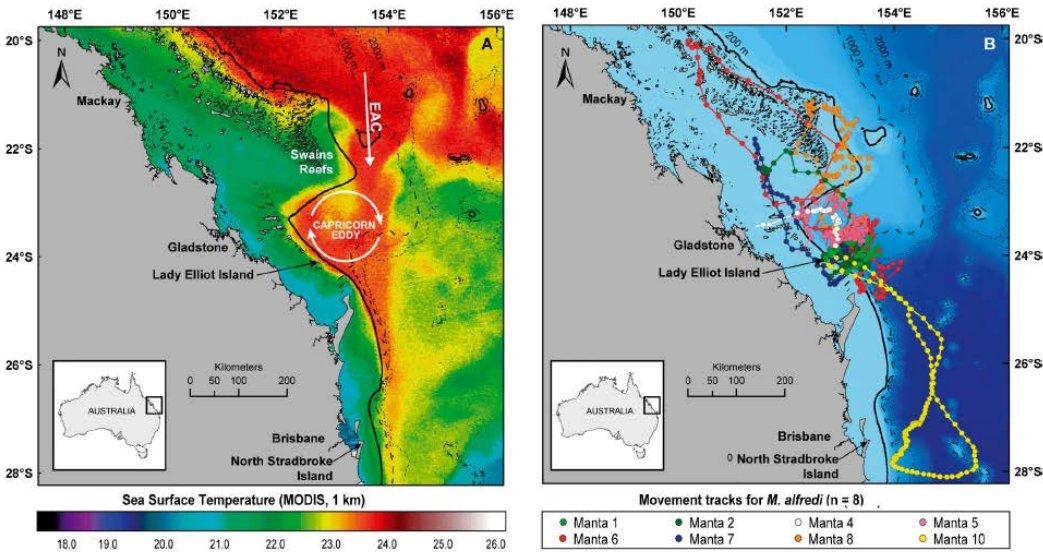


Figure 4. Movements of tagged *Manta alfredi* individuals ($n=8$) off Lady Elliot Island, Great Barrier Reef, Australia, and in relation to the Capricorn Eddy (EAC = East Australian Current). Source: Jaine et al. (2014)

These migrations are largely thought to be feeding-related, influenced by the seasonal distribution of prey. For example, within the Maldives, *M. alfredi* conducts seasonal migrations that correspond to the biannual reversal of monsoon currents (Anderson et al. 2011a). Based on diver and fishermen observations, reef mantas tend to occur on the downstream side of the atolls. As the monsoon currents change direction throughout the year (with the southwest monsoon, where currents flow to the east, lasting from May to October, and the northeast monsoon, where currents flow to the west, from December to March), the mantas tend to migrate in order to remain on the downstream side of the atoll (Anderson et al. 2011a). It is thought that the mantas are following their prey as these areas tend to be where the monsoon currents lift nutrient-rich waters to the surface, resulting in phytoplankton blooms that likely support abundant zooplankton populations (Anderson et al. 2011a). In addition to the Maldives, seasonal aggregations of *M. alfredi* have been documented off Maui, Hawaii (Deakos et al. 2011), Lady Elliott Island, Australia (Couturier et al. 2014), Ningaloo reef, Western Australia (McGregor et al. 2008), and southern Mozambique (Marshall et al. 2011c; Rohner et al. 2013).

Despite the evidence of extensive movements, as noted above, reef manta rays display some degree of site fidelity, returning to known aggregation sites (Couturier et al. 2011;

Deakos et al. 2011; Papastamatiou et al. 2012; Jaine et al. 2014). For example, a pop-up satellite archival tagging (PSAT) study conducted in the Red Sea revealed that although *M. alfredi* may travel along the coastal reef matrix up to 70 km to the south, they continued to return to the same areas of high occupancy (Braun et al. 2015). Along the east coast of Australia, mark-recapture methods and photographic identification of reef manta rays from 1982 to 2012 revealed a re-sighting rate of more than 60% (with females more likely to be resighted than males), suggesting high site fidelity to aggregation sites, including several locations within a range of up to 650 km (Couturier et al. 2014). In Hawaii, 76% of 105 *M. alfredi* individuals observed over 15 years of surveys were re-sighted along the Kona coast, also confirming the high site fidelity behavior of the species (Clark 2010).

In terms of habitat use, *M. alfredi*, similar to *M. birostris*, are considered a link between epipelagic and mesopelagic habitats as they are often found in the upper 10 m of their habitat during the day (near reef cleaning stations and feeding grounds) but can dive to depths of up to 432 m at night (Clark 2010; Braun et al. 2014). While this diving behavior is thought to be associated with manta ray feeding, particularly on the rich zooplankton layers deeper and farther out in the ocean (Jaine et al. 2014), Braun et al. (2014) also observed gliding dive movements made by *M. alfredi*, which the authors hypothesized are potentially used as a means of energy-efficient travel for the species.

Feeding and Diet

Both manta species primarily feed on planktonic organisms such as euphausiids, copepods, mysids, decapod larvae and shrimp, but some studies have noted their consumption of small and moderate sized fishes as well (Bertolini 1933; Bigelow and Schroeder 1953; Carpenter and Niem 2001; The Hawaii Association for Marine Education and Research Inc. 2005; Rohner et al. 2017a; Stewart et al. 2017). For example, Rohner et al. (2017a) documented two species of myctophid fishes (*Myctophum asperum* and *My. Spinosum*) in the stomach contents of *M. birostris* in the Bohol Sea (Philippines). Hartup et al. (2013) also documented reef manta rays feeding on surgeonfish spawn aggregations, with the number of mantas correlated with the size of the spawn aggregation. However, planktonic organisms appear to comprise the majority of the diet for these two species and may influence their feeding habits. In fact, captive mantas (identified as *M. alfredi* from

photographs) were reported to consume 12.7% of their body weight in euphausiids weekly (Homma et al. 1999). The appearance of feeding *M. alfredi* at Lady Elliot Island was correlated with significantly greater zooplankton abundance (2547 m^{-3}) and biomass (19.12 mg m^{-3}) than what was estimated during times when mantas were not feeding or were absent (648 m^{-3} and 906 m^{-3} ; 9.33 mg m^{-3} and 8.59 mg m^{-3} , respectively) (Armstrong et al. 2016). Similarly, off Kona, Hawaii, a significant positive correlation was found between manta ray numbers and zooplankton abundance (Osada 2010). Size of individuals within the zooplankton community did not impact the likelihood of manta ray feeding behavior, suggesting that manta feeding habits are likely influenced by the movement and accumulation of zooplankton (Armstrong et al. 2016). Additionally, based on observations and diet analyses of *M. birostris* off Peru, Sri Lanka, and the Philippines, Stewart et al. (2017) found that both juvenile and adult manta rays target the same prey, and, thus, likely occupy the same habitats within a location.

However, while it was previously assumed, based on field observations, that manta rays feed predominantly during the day on surface zooplankton, results from recent studies (Couturier et al. 2013; Burgess et al. 2016) indicate that these feeding events are not an important source of the dietary intake for these two species. For *M. alfredi*, Couturier et al. (2013) used stable isotope and signature fatty acid analyses of muscle tissues from individuals collected off Queensland, Australia and southern Mozambique to examine the reef manta ray diet. The results indicated that demersal zooplankton likely comprise an important component of the species' diet (Couturier et al. 2013). The trophic position for *M. alfredi* was estimated to be around 3, making it a secondary consumer (Couturier et al. 2013). The authors suggest that reef manta rays are nocturnal feeders, targeting demersal zooplankton as they emerge from the sediment and migrate upwards at night (Cushing 1951; Forward 1988; Couturier et al. 2013). For *M. birostris*, Burgess et al. (2016) used stable isotope analysis of muscle tissues of individuals collected off Ecuador and surface zooplankton to examine the giant manta ray diet. The authors found that, on average, mesopelagic sources contributed 73% to the giant manta ray's diet, compared to 27% for surface zooplankton (Burgess et al. 2016). The results also indicated that *M. birostris* has a trophic position of approximately 3.4, making it a secondary consumer, similar to *M. alfredi*

(Burgess et al. 2016). Overall, both of these studies indicate that manta rays have a more complex depth profile of their foraging habitat than previously thought, and may actually be supplementing their diet with the observed opportunistic feeding in near-surface waters (Couturier et al. 2013; Burgess et al. 2016).

The feeding behaviors of manta species have also been studied to provide insight into their cognition and response to sensory stimuli. When feeding, groups of mantas hold their cephalic fins in an “o” shape and open their mouths wide. They tend to swim at a speed around 30 pectoral fin beats per minute when feeding, which is almost twice as fast as they swim when being cleaned (Kitchen-Wheeler 2013). After collecting water with zooplankton in their mouths, mantas use a transverse curtain on the roof of the mouth as a valve to hold the water in as the pharynx contracts during swallowing (Bigelow and Schroeder 1953). This movement of the pharynx pulls plankton towards the stomach when the gills are closed (Kitchen-Wheeler 2013). Intestinal eversion was also observed, probably to clear the intestines of indigestible material and parasites (Clark and Papastamatiou 2008). The positioning of the cephalic fins was found to be a good indicator of feeding motivation, triggered by underwater visual stimuli or olfactory stimuli (Ari and Correia 2008). Captive mantas seemed to be able to create a cognitive spatial map in their memories that allowed them to return to areas where they remembered being fed (Ari and Correia 2008). Known manta feeding areas that have been reported in the literature are summarized below (**Table 1**); however, it is likely that additional feeding areas exist throughout the species’ respective ranges.

Table 1. Locations of observed feeding areas for both *Manta birostris* and *Manta alfredi*, with site-specific details regarding timing and distribution of the species at these locations.

Source	Location	Site Specifics
<i>M. birostris</i>		
(Clark 2002)	Pacific Ocean	- High site fidelity at Fiji, French Frigate Shoals, Hawaii (all with high plankton abundance)
(Clark 2010)	Hawaii (Big Island)	- Along the Kona Coast
(De Boer et al. 2015)	Suriname Coast	- Coastal waters off Suriname, particularly during rainy season
(Wilson et al. 2001)	Western Australian Coast	- Observed feeding in surge channels at Ningaloo Reef (possibly <i>M. alfredi</i> ?)
(MantaMatcher 2016)	Thailand	- West coast off Khao Lak and Koh Lanta

Source	Location	Site Specifics
(Duffy and Abbott 2003)	New Zealand	- 1999 manta recorded somersault feeding between Nine Pin and Cavalli Islands - 2001 (March) manta recorded somersault feeding 7 km west of Poor Knights Islands on euphausiids; (April) two mantas recorded somersault feeding between Hen & Chickens and Mokohinau Islands
(Girondot et al. 2015)	French Guiana waters	- Peak between July and December when primary production is high
(Graham et al. 2012)	Gulf of Mexico	- Southern Gulf of Mexico near Yucatan Peninsula
(Luiz et al. 2009)	Brazil	- Laje de Santos Marine State Park during austral winter (June-Sept)
(Notarbartolo-di-Sciara and Hillyer 1989)	Venezuela Caribbean Sea	- Between Puerto la Cruz and Isla Margarita (Mar-Dec)
(Stewart et al. 2016b)	Pacific Ocean	- Revillagigedo Archipelago, Mexico year round with seasonal shifts in habitat use probably corresponding to plankton movement
(Mejia-Falla et al. 2014)	Eastern Pacific Ocean	- Gorgona Island National Natural Park, Colombia (March – September)
<i>M. alfredi</i>		
(Anderson et al. 2011a)	Maldives	- Upstream side of Lhaviyani Atoll (Feb/March) - During SW monsoon (April), near Lankanfinolhu Island; during NE monsoon (Nov/Dec), near Embudu Island; during NE monsoon (Nov/Dec), Haa Dhaalu Atoll and Haa Alifu Atoll - Both seasons, Haa Dhaalu Atoll and Shaviyani Atoll
(Dewar et al. 2008)	Indonesia	- Komodo Marine Park
(Armstrong et al. 2016)	Great Barrier Reef	- Lady Elliot Island during high zooplankton biomass (ebb to low tide); largest known aggregation site off eastern Australia
(Braun et al. 2014)	Eastern Red Sea	- Near Al Lith (Saudi Arabia), mantas remained in shallow water during the day and moved to deeper water at night, consistent with observations of zooplankton movement
(Clark 2010; Deakos et al. 2011)	Hawaii	- High site fidelity to Keauhou and Ho'ona Bay, along with movements along the coast and some feeding at Makolea Point; nocturnal foraging in Mahaiula Bay (Big Island) - Aggregation area off west coast of Maui
(Couturier et al. 2011)	Eastern Australian Coast	- Near Lady Elliot Island (peaks in Jun/Jul), North Stradbroke Island (Oct-April), Byron Bay (Feb-April)
(Jaine et al. 2012)	Great Barrier Reef	- Near Lady Elliot Island concentrated along tidal slicks in winter
(Kashiwagi et al. 2011; Venables 2013)	Western Australian Coast	- Bateman Bay, around inner reef sites year round

Source	Location	Site Specifics
(Homma et al. 1999)	Indo-Pacific Ocean	- Yap Island at Manta Ray Hotel (plankton are attracted to lights at night), Yaeyama Islands
(Hartup et al. 2013; Martin et al. 2015)	Guam	- Tumon Bay Marine Preserve, associated with surgeonfish spawning aggregations
(Papastamatiou et al. 2012; McCauley et al. 2014)	Pacific Ocean	- Palmyra Atoll (focusing on lagoons)
(Sleeman et al. 2007; McGregor et al. 2008)	Western Australian Coast	- Ningaloo Marine Park, near Coral Bay

Reproduction and Growth

Carrier et al. (2004) and Hamlett (2005) summarized elasmobranch reproduction. All elasmobranchs have internal fertilization and can be divided further into two groups: oviparous (egg-laying) and viviparous (live-bearing forms). Myliobatiformes like mobulids are viviparous and reproduce most commonly by histotrophy. This is a type of matrotrophy (involving maternal input of nutrients to fetus) where the female produces lipid-rich histotroph (sometimes called uterine milk) for the embryos to consume via long villi called trophonemata (Alcock 1892; Amoroso 1960). This method of reproduction was confirmed in *M. birostris* by White et al. (2006) and, due to maternal nutrition having an effect on embryo development through the histotroph (Tomita et al. 2012), suggests the mother's health will impact fetal development. Reports of manta ray births and dissections have all revealed only a single embryo (Homma et al. 1999; Uchida et al. 2008). Female manta rays have a simple cloaca opening between their paired pelvic fins. Males may be identified by the presence of a pair of claspers extending from the pelvic fins (Kitchen-Wheeler 2013).

Male *M. alfredi* in the Maldives were observed to court females either by exhibiting shadowing or chasing behavior. Chasing behavior simply referred to the males swimming behind the female in a mating train, but shadowing behavior involved the male positioning himself parallel to and above the female's dorsal surface whilst stimulating her dorsal surface with his cephalic fins. Kitchen-Wheeler (2013) observed that shadowing behavior was common throughout the year but was less likely to lead to mating, while chasing

behavior was only recorded during mating seasons. In the Maldives, two primary mating seasons were recorded based on numbers of pregnant mantas: October-November and February-March. Pectoral fin scars on females, primarily on the left wing, were seen to result from the male biting the female while he inserted a clasper into her cloaca for insemination (Deakos 2012; Kitchen-Wheeler 2013). Yano et al. (1999b) reported that *M. birostris* near the Ogasawara Islands (Japan) were seen engaging in “mating trains,” where multiple males pursue a single female. They recorded the primary breeding season of *M. birostris* as July-August. Deakos (2012) confirmed the presence of similar behavior in *M. alfredi* off Maui, Hawaii as well, but the majority of pregnant females were observed during the winter months (November – April). *Manta birostris* breeding sites have also been identified off the coast of Ecuador and in the Galapagos Islands, with pregnant females observed off Isla de la Plata in the Machalilla National Park and Galapagos Marine Reserve (Hearn et al. 2014). The mating displays can last hours or days, with the female swimming rapidly ahead of the males and occasionally somersaulting or turning abruptly (Deakos et al. 2011). Males were never observed to compete with each other directly for the attention of the female, so these mating trains may function as a kind of endurance rivalry (Andersson 1994; Deakos 2012). No copulations have been observed in the wild, so it is difficult to determine which males have a mating advantage, but this kind of endurance trial usually selects for the success of larger males (Andersson and Iwasa 1996; Deakos 2012). As for the differences in mating season, seasonal breeding is usually due to some kind of advantage like food availability or predation pressure for the pup when it is born; this may vary by region.

The female manta appears to choose her mate based on these mating displays. Sexual dimorphism is present in manta rays, with female *M. alfredi* as much as 18% larger than males, so it is unlikely that a male could force a female to mate against her will (Deakos 2010b; Marshall and Bennett 2010b). Females also put more effort into nourishing the offspring than the male, and thus are expected to be the choosier sex (Trivers 1972). Deakos (2012) recorded an occurrence of a female *M. alfredi* observed mating both 16 and 14 months before she was observed to be visibly pregnant. Because gestation appears to last 12-13 months, it therefore appears all mating attempts do not result in conception and

females may have multiple ovulations per year if they do not become pregnant on their first mating attempt. It may be assumed that females leading a mating train are ovulating, as males in the mating trains were observed to ignore other adult females in the area aside from briefly investigating behind the females. Ari and Correia (2008) have already recorded *M. birostris* using its acute sense of smell to locate food, while others have recorded male elasmobranchs using scent to identify if females are receptive to mating, so it seems safe to assume that these females leading the mating trains are indeed ovulating (Johnson and Nelson 1978; Gordon 1993).

Statistically significant female-biased female to male sex ratios are observed in many reef manta ray aggregations (1.3:1 in Australia, 1.8:1 in the Maldives, and 3.5:1 in Mozambique) (Couturier et al. 2011; Marshall et al. 2011c; Kitchen-Wheeler 2013; Venables 2013). However, the reef manta ray population off Maui, Hawaii appears to be only slightly skewed and towards males, with a sex ratio of 1:1.34 (Deakos 2010b; Deakos 2012). Given biennial mating (with an estimated mean pregnancy rate of 0.56 pups per year), the number of reproductively available females in this Maui population would be reduced by half, inflating the operational sex ratio to 2.68 adult males per female (Deakos 2012). Deakos (2011) hypothesized that the different sex ratios of the Maui population compared to other *M. alfredi* populations may be due to the Maui location being farther from a suitable pupping ground. However, at this time, locations of manta ray pupping and nursery grounds for both species remain unknown. The lack of observations of small manta rays throughout the species' respective ranges may indicate that manta rays segregate by size, with different habitats potentially used by neonates and juveniles (Deakos 2010b). While these habitats have yet to be identified, Erdmann (2014) presents a hypothesis, based on tagging data of a juvenile *M. alfredi* (~1.5m DW), that mantas likely give birth in protected areas, such as lagoons, that provide protection from larger predators. The reef manta ray, who was tagged and tracked in late June of 2014 in Wayag lagoon in northern Raja Ampat, spent 95% of its time within the lagoon, only venturing out a few times into the deeper waters surrounding the lagoon, potentially to feed (Erdmann 2014).

Not much is known about manta growth and development. A 4.0 m DW captive *M. alfredi* was observed to give birth to a 1.92 m DW neonate 374 days after she was observed mating. After mating again, she gave birth to a 1.82 m DW neonate after a 368-day gestation period (Matsumoto and Uchida 2008; Uchida et al. 2008). Another captive manta ray (identified as *M. birostris*) gave birth to a 1.8 m DW 66 kg neonate (Okinawa Churaumi Aquarium cited in Deakos 2012). A 1.14 m DW neonate, weighing 9.8 kg, was collected from a landed pregnant reef manta ray off Kochi, India (Nair et al. 2015). Free swimming wild mantas have also been observed as small as 1.02 m DW and 1.22 m DW, so it is likely these young mantas are representative of a normal wild birth size with gestation period around a year. The young mantas were only able to swim properly after a few minutes when their wings fully unfurled, meaning that neonates would be at risk for predation during this time. Thus, the mother's choice of birth site may make a difference in survival rate (Berriman 2007; Kitchen-Wheeler 2013) as mantas do not provide any parental care to their offspring after birth.

In *M. alfredi*, Deakos (2012) observed that sexual maturity was delayed until growth had reached 90% of maximum size, pointing to large body size providing a reproductive advantage. Deakos (2010b) concluded that the minimum size at sexual maturity was 3.37 DW for female *M. alfredi* and 2.80 m DW for males in Maui. In the Maldives, Kitchen-Wheeler (2013) observed a pregnant female *M. alfredi* at a size of 4.1 m DW and a mature male at a size of 3.7 m DW. There is no evidence that male size affects mating success of *M. alfredi* in any way (except perhaps indirectly by increasing endurance in mating trains), but larger females were observed to have higher rates of pregnancy than smaller females (Deakos 2012). Homma et al. (1999) hypothesized that age at sexual maturity was 8-13 years in mantas and the data of Uchida et al. (2008), Marshall et al. (2011a) and Marshall and Bennett (2010b) confirmed this estimate. However, a population of female *M. alfredi* in the Maldives displayed late maturity (15 years or more) and lower reproductive rates than previously reported (one pup every five years, instead of biennially) (G. Stevens in prep. as cited in CITES (2013)). In contrast, Clark (2010) described a rapid transition to maturity for *M. alfredi* in Kona, Hawaii, with estimates of males reaching sexual maturity as early as 3-4 years. Although mantas have been reported to live to at least 40 years old (Marshall

and Bennett 2010b; Marshall et al. 2011b; Kitchen-Wheeler 2013) with low rates of natural mortality (Couturier et al. 2012), the time needed to grow to maturity and the low reproductive rates mean that a female will be able to produce only 5-15 pups in her lifetime (CITES 2013). Generation time for both species (based on *M. alfredi* life history parameters) is estimated to be 25 years (Marshall et al. 2011a; Marshall et al. 2011b).

Known life history characteristics of *M. birostris* and *M. alfredi* are summarized below in **Table 2** and **Table 3**.

Table 2. Available life history parameters for *Manta birostris* (f = female; m = male; DW = Disc Width).

Ocean Basin (Sampled Location)	Maximum DW (meters)	Weight (observed; kg)	Maximum Age (years; observed)	DW at Maturity (meters)	Age at maturity (years; observed)	Litter Size	DW at Birth (meters)	Weight at Birth (kg)	Reference
Western North Atlantic	6.7	1,360			4.3-4.6 (f) >3.5 (m)	1	1.14	12.7	Bigelow and Schroeder (1953)
Indian	6.8 (f)	2,400 (f)			>4.1 (f) >3.8 (m)				Kunjipalu and Boopendranath (1982); White et al. (2006); Nair et al. (2015)
Indian (Mozambique)	>7		>40	>4.7 (f) 4 (m)					Marshall et al. (2009)
Indo-Pacific (Bohol Sea, Philippines)	5.52 (f) 4.46 (m)								Rohner et al. (2017a)
Pacific (Japan)	5 4.65 (f)	774							Yanagisawa (1994) and Uchida (1994) cited in Deakos (2010a)
Pacific (Peru)	6-7	~1,000							Main (2015)

Table 3. Available life history parameters for *Manta alfredi* (f = female; m = male; DW = Disc Width).

Sampled Location	Maximum DW (meters)	Maximum Age (years; observed)	DW at Maturity (meters)	Age at maturity (years; observed)	Litter Size	DW at Birth (meters)	Weight at Birth (kg)	Gestation (days)	Reproductive Periodicity	Reference
Indian (South Africa)	4.9	>40		Female 8-10 (f)	1	1.5, 1.3				Marshall et al. (2008); Marshall et al. (2009)

Sampled Location	Maximum DW (meters)	Maximum Age (years; observed)	DW at Maturity (meters)	Age at maturity (years; observed)	Litter Size	DW at Birth (meters)	Weight at Birth (kg)	Gestation (days)	Reproductive Periodicity	Reference
Indian (Mozambique)			>3.9 (f) >3 (m)		1-2	1.5, 1.67		365+ (374, 368)	1-3 year cycle	Marshall and Bennett (2010b)
Indian (Maldives)	4.5 (f) 4.0 (m)	>36		>15	1				1-2 year cycle 5 year cycle	Kitchen-Wheeler (2013); G. Stevens unpub. data cited in Anderson et al. 2011b; G. Stevens in prep cited in CITES (2013)
Indo-Pacific (Indonesia)			>4.13 (f) >3.75 (m)							White et al. (2006)
Pacific (Japan)	4.3 (f) 3.6 (m)	>27	3.8-4 (f) 2.8-3.0 (m)	9-16 (f) 4-9 (m)	1	0.9 - 1.92	68.5	368 - 374	3-4 year cycle	Kashiwagi et al. (2008) Kashiwagi (2014); Matsumoto and Uchida (2008)
Pacific (Yap)	4.67	>20							2-3 year cycle	Homma et al. (1999)
Pacific (Australia)	4-4.5 (f)	>30	~3.5 (m)							Couturier et al. (2014)
Pacific (Hawaii)	3.37 (f) 2.8 (m)		3.37 (f) 2.75 (m)	3-6 (m)						Deakos (2010b)

Population Structure

Since the splitting of the Manta genus, most of the recent research has examined the genetic discreteness, phylogeny and the evolutionary speciation in manta rays (Cerutti-Pereyra et al. 2012; Kashiwagi et al. 2012; Poortvliet et al. 2015). Very few studies have focused on the population structure within each species. However, based on genetic sampling, photo-identification and tracking studies, preliminary results tend to indicate that reef manta rays exist in isolated and potentially genetically divergent populations. For example, using genetic sequencing of 550 base pairs of the mitochondrial COI gene (i.e., the barcoding gene) from tissue samples of four manta ray individuals, Cerutti-Pereyra et al. (2012) found low genetic divergence (<1%) but “phylogeographic disjunction” between *M. alfredi* samples from Australia (n=2; Ningaloo Reef) and Indonesia (n=2), suggesting biogeographic factors may be responsible for population differentiation within the species. Although based on very few samples, these findings are further supported by photo-identification and tracking studies, which suggest high site-fidelity and residency for *M. alfredi* in many portions of its range, including Indonesia, Ningaloo Reef, Hawaii, Fiji, New Caledonia, and eastern Australia (Dewar et al. 2008; Clark 2010; Couturier et al. 2011; Deakos et al. 2011; Cerutti-Pereyra et al. 2012; Couturier et al. 2014). In Hawaii, for example, Clark (2010) used photo-identification survey data collected between 1992 and 2007 and discovery curves to analyze the population structure of *M. alfredi* along the Kona coast, with results that showed a constant low rate of immigration for *M. alfredi*, indicating a likely closed population. Additionally, 75% of identified *M. alfredi* individuals were re-sighted multiple times within the study area over the 15-year period, and some individuals were also sighted at a manta cleaning station 28 km north of the study site. Given the high re-sighting rates of *M. alfredi* coupled with the low immigration rate, the authors concluded that the reef manta rays along the entire coast of Hawaii likely constitute a single population.

The population structure for the wider-ranging *M. birostris* is less clear. While the Clark (2010) study found low site-fidelity for *M. birostris* and much higher rate of immigration, indicative of a population that is pelagic rather than coastal or island-associated, Stewart et al. (2016a) provided recent evidence to show that the giant manta rays off Pacific Mexico

may exist as isolated subpopulations, with distinct home ranges. Additionally, researchers are presently investigating whether there is a potential third manta ray species resident to the Yucatán coastal waters of the Gulf of Mexico (previously identified as *M. birostris*) (Hinojosa-Alvarez et al. 2016). Using the mitochondrial *ND5* region (maternally-inherited DNA), Hinojosa-Alvarez et al. (2016) found shared haplotypes between Yucatán manta ray samples and known *M. birostris* samples from Mozambique, Indonesia, Japan, and Mexico, but discovered four new manta ray haplotypes, exclusive to the Yucatán samples. While analysis using the nuclear *RAG1* gene (bi-parentally-inherited DNA) showed the Yucatan samples to be consistent with identified *M. birostris* sampled, the authors suggest that the *ND5* genetic evidence indicates the potential for a third, distinctive manta genetic group or possibly *M. birostris* subspecies. At this time, additional studies, including in-depth taxonomic studies and additional genetic sampling, are needed to better understand the population structure of both species throughout their respective ranges.

Population Demographics

Given their large sizes, manta rays are assumed to have fairly high survival rates after maturity (e.g., low natural predation rates). In fact, Couturier et al. (2014) estimated annual survival of *M. alfredi* at Lady Elliott Island, Australia to be near 1 for both sexes (based on mainly large, mature individuals). Similarly, Deakos et al. (2011) estimated rates of 0.948 to 1 for annual survival for the *M. alfredi* population off Maui, Hawaii, and Kashiwagi (2014) calculated this rate to be 0.95 for the reef manta ray population off the Yaeyama Islands, Japan. In contrast, the annual survival of the *M. alfredi* population off Mozambique was estimated to be substantially lower, between 0.6-0.7; however, shark attacks appear to be more common in this portion of the species' range compared to the other areas (Marshall et al. 2011c).

Using estimates of known life history parameters for both giant and reef manta rays, and plausible range estimates for the unknown life history parameters, Dulvy et al. (2014) calculated a maximum population growth rate of *Manta* spp. and found it to be one of the lowest values when compared to 106 other shark and ray species. Specifically, the median maximum population growth rate (R_{max}) was estimated to be 0.116, a rate that is more similar to those calculated for marine mammal species than chondrichthyan species (Dulvy

et al. 2014; Croll et al. 2015). After taking into consideration different model assumptions, and the criteria for assessing productivity in Musick (1999), Dulvy et al. (2014) estimated realized productivity (r) for manta rays to be 0.029 (Dulvy et al. 2014). This value is similar to the productivity estimate from Kashiwagi (2014) who empirically determined an r value of 0.023 using capture-mark-recapture analyses. Ward-Paige et al. (2013) calculated slightly higher estimates for the intrinsic rate of population increase, with $r = 0.05$ for *M. alfredi* and $r = 0.042$ for *M. birostris*; however, these estimates still place both manta ray species into the “very low” productivity category ($r < 0.05$), based on the productivity parameters and criteria in Musick (1999).

In order to determine how changes in survival may affect populations, Smallegange et al. (2016) modeled the demographics of reef manta rays. In their own observations of the population off the southern coast of Mozambique, the authors estimated an adult survival rate of 0.67 (± 0.16 SE). Results from the population modeling (based on *M. alfredi* demographics) showed that increases in yearling or adult annual survival rates resulted in much greater responses in population growth rates, mean lifetime reproductive success, and cohort generation time compared to similar increases in juvenile annual survival rates (Smallegange et al. 2016). Based on the elasticity analysis, population growth rate was most sensitive to changes in the survival rate of adults (Smallegange et al. 2016). In other words, in order to prevent populations from declining further, Smallegange et al. (2016) found that adult survival rates should be increased, such as through protection of adult aggregation sites or a reduction in fishing of adult manta rays (Smallegange et al. 2016). For those populations that are currently stable, like the Yaeyama Islands (Japan) population (where adult annual survival rate is estimated at 0.95; noted above), Smallegange et al. (2016) note that any changes in adult survival may significantly affect the population.

Overall, given their life history traits and productivity estimates, particularly their low reproductive output and sensitivity to changes in adult survival rates, giant and reef manta ray populations are inherently vulnerable to depletions, with low likelihood of recovery.

HISTORICAL AND CURRENT ABUNDANCE AND TRENDS

M. birostris

There are no current or historical estimates of the global abundance of *M. birostris*. Despite their larger range, they are encountered with less frequency than *M. alfredi*. Most estimates of subpopulations are based on anecdotal diver or fisherman observations, which are subject to bias. These populations seem to potentially range from around 100-1,500 individuals (**Table 4**). The Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) (2013) reports that because 10 populations of *M. birostris* have been actively studied, 25 other aggregations have been anecdotally identified, and all other sightings are rare, the total global population may be small. The greatest number of *M. birostris* identified in the four largest known aggregation sites ranges from 180 to 1,500 (**Table 4**). Ecuador is thought to be home to the largest identified population of *M. birostris* in the world, with large aggregation sites within the waters of the Machalilla National Park and the Galapagos Marine Reserve (Hearn et al. 2014). Within the Indian Ocean, numbers of giant manta rays identified through citizen science in Thailand's waters (primarily on the west coast, off Khao Lak and Koh Lanta) have been increasing over the past few years, from 108 in 2015 to 288 in 2016. These numbers reportedly surpass the estimate of identified giant mantas in Mozambique (n=254), possibly indicating that Thailand may be home to the largest aggregation of giant manta rays within the Indian Ocean (MantaMatcher 2016). In the Atlantic, very little information on *M. birostris* populations is available. Based on personal observation during aerial surveys conducted off of St. Augustine, Florida, from 2009-2012, F. Young (pers. comm. 2017) noted vast schools of giant manta rays, with over 500 manta rays observed per 6-8 hour day of aerial survey. There is also a known, protected population of manta rays within the Flower Garden Banks National Marine Sanctuary in the Gulf of Mexico. However, researchers are still trying to determine whether the manta rays in this area are only *M. birostris* individuals or potentially also comprise individuals of a new, undescribed species (Marshall et al. 2009; Hinojosa-Alvarez et al. 2016).

Table 4. Numbers of recorded individuals and subpopulation estimates of *Manta birostris* at identified locations adapted from CITES (2013).

Location	Recorded Individuals	Subpopulation Estimate	Reference
Mozambique	180 - 254	600	Marshall et al. (2009) & pers. comm. cited in CITES (2013); MantaMatcher (2016)
Egypt	60	-	Marine Megafauna Foundation unpubl. cited in CITES (2013)
Republic of Maldives	63	-	G. Stevens, pers. comm. cited in CITES (2013)
Kona, Hawaii	29		Clark (2010)
Thailand	>288	-	MantaMatcher (2016)
Raja Ampat, Indonesia	72	-	MMP & The Manta Trust, unpubl. cited in CITES (2013)
Isla de la Plata, Ecuador	~650	1,500	M. Harding, pers. comm. cited in CITES (2013); Sanchez (2016)
Brazil	60	-	Laje Viva Institute unpubl. cited in CITES (2013), Luiz et al. (2009)
Mexico (Revillagigedos Is.)	412	-	R. Rubin & K. Kumli, pers. comm. cited in CITES (2013)
Mexico (Isla Holbox)	> 200	-	R. Graham, pers. comm. cited in CITES (2013)
Flower Garden Banks	>70	-	Graham and Witt (2008) cited in CITES (2013)
St. Augustine, Florida	90 - >500		Kendall (2010); F. Young, pers. comm. (2017)
Japan (Ogasawara Islands)	42	-	Kashiwagi et al. (2010)

In areas where the species is not subject to fishing, populations may be stable. However, in regions where giant manta rays are (or were) actively targeted or caught as bycatch, such as the Philippines, Mexico, Sri Lanka, and Indonesia, populations appear to be decreasing (**Table 5**). In Indonesia, declines in manta ray landings are estimated to be on the order of 71% to 95%, with potential extirpations noted in certain areas (Lewis et al. 2015). Given the migratory nature of the species, population declines in waters where mantas are protected have also been observed but attributed to overfishing of the species in adjacent

areas within its large home range. For example, White et al. (2015) provide evidence of a substantial decline in the *M. birostris* population in Cocos Island National Park, Costa Rica, where protections for the species have existed for over 20 years. Using a standardized time series of observations collected by dive masters on 27,527 dives conducted from 1993 to 2013, giant manta ray relative abundance declined by approximately 89% (95% CI 85-92%) (**Figure 5**). Years of higher abundance of the species were correlated with lower El Niño activity. However, based on the frequency of the species' presence on dives (4%), with a maximum of 15 individuals observed on a single dive, the authors suggest that Cocos Island may not be a large aggregating spot for the species, and suggest that the decline observed in the population is likely due to overfishing of the species outside of the National Park (White et al. 2015).

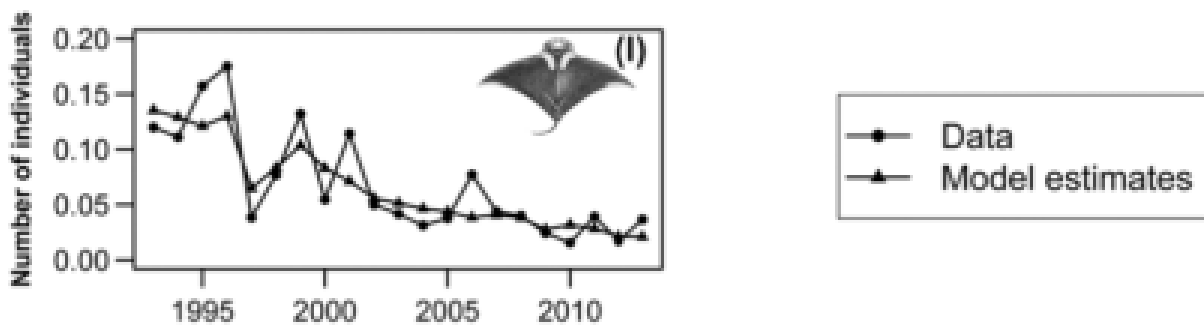


Figure 5. Observed and modeled estimates of mean annual numbers of *Manta birostris* individuals in Cocos Island National Park, based on diver observations from 1993 to 2015. Source: White et al. (2015)

Table 5. Observed and anecdotal declines in manta ray populations, reported by area. Methodology, time period, notes, and sources of reported declines are also provided. Adapted from CITES (2013).

Area	Species	Time Period	Methodology	% Decline	Notes	Source(s)
Indonesia (throughout)	<i>Manta spp.</i> (likely <i>M. birostris</i>)	2001-2014 (13 years of data provided)	Historical and current landings from published literature, unpublished data from anecdotal reports, field surveys, casual and semi-structured interviews, direct observations	71-95% (landings) Potential areas of extirpation based on anecdotal reports include Lembeh Strait and Selayar Islands.	Shift in fishing grounds due to declining catches of manta rays	Dewar (2002); Setiasih et al in prep. cited in CITES (2013); White et al. (2006); Lewis et al. (2015)
Indonesia (Alor Island)	<i>M. alfredi</i>	2003-2013 (general - over past 10 years)	Anecdotal reports from fishermen	Potential area of extirpation off the west coast of Alor Island	Caught as bycatch in drift gillnets in channel, no longer seen	Lewis et al. (2015)
Indonesia (Komodo National Park)	<i>M. alfredi</i>		Anecdotal reports from local dive operators and park rangers	Unknown	Observed decline in abundance	Dewar (pers comm.) cited in CITES (2013)
Bohol Sea, Philippines	<i>Manta spp.</i> (likely <i>M. birostris</i>)	1990s – 1997 (general - memory recall of 1990s data)	Standardized questionnaire to artisanal fishermen (n=85) to assess catch and effort	Unknown	15% of fishermen noted a decrease in landings of whale shark/manta resources	Alava et al. (2002)

Area	Species	Time Period	Methodology	% Decline	Notes	Source(s)
Bohol Sea, Philippines	<i>Manta spp.</i> (likely <i>M. birostris</i>)	1997 – 2013 (general - memory recall of previous years)	Interviews with fishermen	Unknown	Shift in fishing grounds due to declining catches of manta rays	Acebes and Tull (2016)
Sulu Sea, Philippines	<i>Manta spp.</i> (possibly <i>M. alfredi</i> ?)	End of 1980s-1990s (general - over past 7 years)	Personal (amateur) scuba diver sightings data	50-67%	Location reported to be off Palawan Island	Michiyo Ishitani, pers. comm. cited in Homma et al. (1999)
S. Mozambique (Inhambane province)	<i>M. alfredi</i>	2003 – 2016 (14 years of data provided)	Scuba diver sightings data – standardized and adjusted to take into account short-term environmental variables	98%	Reef manta rays actively fished, with around 20-50 killed annually along 50 km of the coastline within the study	Rohner et al. (2013); Rohner et al. (2017b)
S. Mozambique (Inhambane province)	<i>M. birostris</i>	2003 – 2016 (14 years of data provided)	Scuba diver sightings data – standardized and adjusted to take into account short-term environmental variables	94%	No clear trend based on data from 2003-2011; however, with expansion of data set to 2016, showed steep decline in observations.	Rohner et al. (2013); Rohner et al. (2017b)

Area	Species	Time Period	Methodology	% Decline	Notes	Source(s)
Thailand	<i>Manta spp.</i> (likely <i>M. birostris</i>)	2006-2012 (2 years of data provided)	Local dive professional detailed sightings data	76%	Sightings of <i>Manta spp.</i> decreased from 59 in 2006-2007 season down to 14 during 2011-2012 season	R. Parker, pers. comm. cited in CITES (2013)
Sri Lanka	<i>M. birostris</i>	2006-2011 (general - over past 5 years)	Interviews with fishermen	Unknown	Decrease in numbers of mantas caught	Fernando and Stevens (2011)
Madagascar	<i>Manta spp.</i>	2003-2013 (general - over past 10 years)	Anecdotal scuba diver and fishermen sighting observations	Unknown	Large decline in sightings	R. Graham, pers. comm. cited in CITES (2013) and pers. comm. (2016)
Yaeyama Islands, Japan	<i>Manta spp.</i> (<i>M. alfredi?</i>)	1980 - 1997 (3 years of data provided)	Local dive professional (T. Itoh) sightings data	Unknown; number of individuals in school decreased from 50 to 14-15	Authors note that while the school size has decreased, this does not necessarily mean that the population abundance has declined; both pregnant females and young were	Homma et al. (1999)

Area	Species	Time Period	Methodology	% Decline	Notes	Source(s)
					part of the school groups	
Papua New Guinea	<i>Manta spp (M. alfredi?)</i>	1994-2006 (12 years of data provided)	Monitored catch and surveys of fishermen	Unknown	Sharp decline noted in bycatch after a prior steady increase from 1994-2005/2006.	C. Rose, pers. comm. cited in Marshall et al. (2011b)
Kiribati	<i>Manta spp.(likely M. alfredi)</i>		Observations by a local dive operator	Unknown	Anecdotal report that the local population has suffered significant declines.	O'Malley et al. (2013)
Cocos Island, Costa Rica	<i>M. birostris</i>	1993 - 2013 (20 years of data provided)	Observations by dive masters	89%	Local dive professional sightings data	White et al. (2015)
Sea of Cortez, Mexico	<i>M. birostris</i>	1981-1992 (2 years of data provided)	Underwater filmmaker observations from 1981 and 1991-1992 film projects	Unknown	Observed 3-4 per dive in 1981 and then zero individuals in 1991-1992	CITES (2013)

Manta alfredi

Given that all manta rays were identified as *M. birostris* prior to 2009, information on the historical abundance and distribution of *M. alfredi* is scarce. CMS (2014) reports that current global population numbers are unknown and no historical baseline data exist. Local populations of *M. alfredi* have not been well assessed either, but appear generally to be small, sparsely distributed, and isolated. Photo-identification studies in Hawaii, Yap, Japan, Indonesia, and the eastern coast of Australia suggest these subpopulations range from 100 to 350 individuals (**Table 6**), despite observational periods that span multiple decades. However, in the Maldives, population estimates range from 3,300 to 9,677 individuals throughout the 26 atolls in the archipelago (Kitchen-Wheeler et al. 2012; CITES 2013; CMS 2014), making it the largest identified population of *M. alfredi* in the world. Other larger populations may exist off southern Mozambique (superpopulation estimate of 802-890 individuals; Rohner et al. (2013); CITES (2013)) and Western Australia (metapopulation estimate = 1,200 – 1,500; McGregor (2009) cited in CITES (2013)).

Table 6. Numbers of recorded individuals and subpopulation estimates of *Manta alfredi* at identified locations adapted from CITES (2013).

Region	Recorded Individuals	Subpopulation Estimate	Reference
Southern Mozambique	685	802 -890 (superpopulation)	Marshall unpubl. cited in CITES (2013), Marshall et al. (2009); Marshall et al. (2011b); Rohner et al. (2013)
Republic of Maldives	2,410; 537 (North Male Atoll)	3,300 - 9,677	CMS (2014); CITES (2013); Kitchen-Wheeler et al. (2012)
Bali, Indonesia	135	-	IMP & The Manta Trust, unpubl. cited in CITES (2013)
Komodo, Indonesia	150	~300	KMP 2011 & The Manta Trust, unpubl. cited in CITES (2013) and Heinrichs et al. (2011)
Raja Ampat, Indonesia	231	-	MMP & The Manta Trust, unpubl. cited in CITES (2013)

Region	Recorded Individuals	Subpopulation Estimate	Reference
Ryukyu Archipelago, Japan	368	-	Kashiwagi et al. (2011)
Yap, Micronesia	100	~100	Marshall et al. (2011b)
Guam	35	-	J. Hartup, pers. comm. cited in CITES (2013)
Palau	170	-	J. Denby & M. Etpison, pers. comm. cited in CITES (2013)
East Coast, Australia (Osprey Reef and South Solitary Island)	620	-	L. Couturier, pers. comm cited in CITES (2013)
Ningaloo Reef, Australia	>800	1,200 – 1,500 (metapopulation) 40 – 50 (resident population at Bateman Bay)	McGregor 2009 – cited in CITES (2013); Venables (2013); Venables et al. (2016)
Bora Bora, French Polynesia	93	-	M. De Rosemont, pers. comm. cited in CITES (2013)
Maui, Hawaii	323	350	M. Deakos, pers. comm. cited in CITES (2013)
Kona, Hawaii	181	-	Manta Pacific Research Foundation 2011 cited in CITES (2013)
Yaeyama Islands, Japan	305	~165-202	Kashiwagi et al. (2010); Kashiwagi (2014)
Lady Elliot Island, Australia	~456 (within one season)	~300	Couturier et al. (2014); K. Townsend pers. comm. cited in CITES (2013)

In terms of trends, studies report that the rate of population reduction appears to be high in local areas, from 50-98%, with areas of potential local extirpations (**Table 5**) (Homma et al. 1999; Rohner et al. 2013; Lewis et al. 2015; Rohner et al. 2017b). In the portions of range where reef mantas are experiencing anthropogenic pressures, including Indonesia and Mozambique, encounter rates have dropped significantly over the last five to ten years (CMS 2014). Recently, Rohner et al. (2017b) demonstrated a decline approaching 98% over a 14 year period in Southern Mozambique, significant as generation time for *M. alfredi* is

estimated to be 25 years (Marshall et al. 2011b). Off the west coast of Alor Island in Indonesia, an *M. alfredi* population disappeared within 5 years after a local village installed drift nets in the middle of the channel separating the Alor and Pantar Islands (Lewis et al. 2015), demonstrating the sensitivity of the species to fishing mortality and the short time that it takes for these populations to become depleted and extirpated.

Where *M. alfredi* receives some kind of protection, such as in Australia, Hawaii, Guam, Japan, the Maldives, Palau, and Yap, CITES (2013) reports that subpopulations are likely to be stable. In Hawaii, based on photo-identification survey data collected between 1992 and 2007 along the Kona Coast, Clark (2010) used a discovery curve to estimate that an average of 4.27 new pups were entering the population per year. Based on aerial surveys of Guam conducted from 1963 to 2012, manta ray observations were infrequent but showed an increase over the study period (**Figure 6**) (Martin et al. 2015).

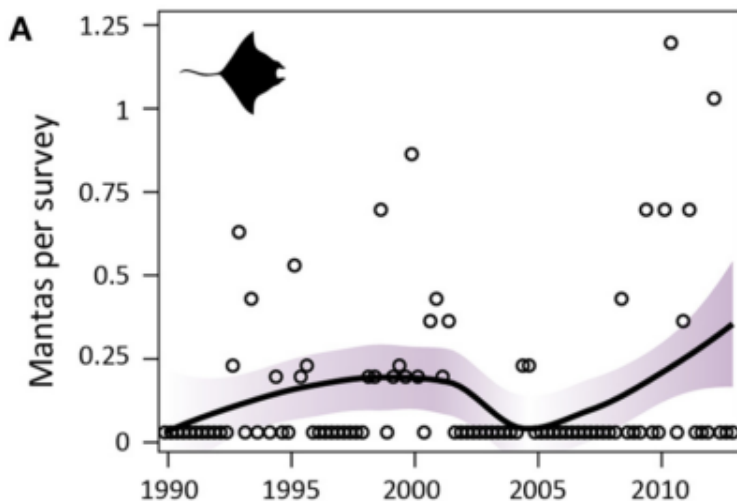


Figure 6. Trend in Manta ray observations from semimonthly aerial surveys over Guam. Shaded area around trend line depicts 95% confidence interval. Source: Martin et al. (2015)

From 2009 to 2012, Couturier et al. (2014) modeled annual population sizes of *M. alfredi* aggregating at Lady Elliott Island, Australia and found an annual increase in abundance for both sexes. While these results may indicate a potential growth of this subpopulation, the authors also caution that the modeled increase could be an artifact of improvements in photo-ID by observers over the study period (with a greater ability to identify all rays at an aggregation site) (Couturier et al. 2014). Within Ningaloo Marine Park, the status of reef manta rays was assessed as “Good” in 2013, but with low confidence in the ratings (Marine

Parks & Reserves Authority 2013). Overall, the reef manta ray population of Australia is deemed to be one of the world's healthiest (Australian Government 2012). Off the Yaeyama Islands, Japan, Kashiwagi (2014) conducted quantitative analyses using encounter records, biological observations, and photo-ID of manta rays over the period of 1987 to 2009 and found that the apparent population size increased steadily but slowly over the 23-year period (**Figure 7**), with a population growth rate estimate of 1.02-1.03.

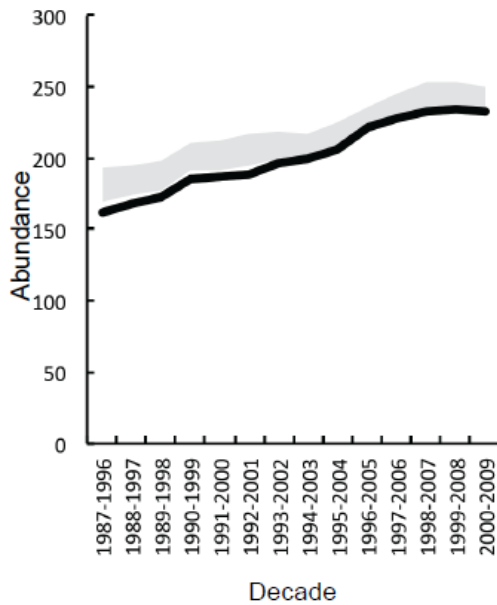


Figure 7. Trend in manta ray population size from 1987-2009 in Yaeyama, Japan. Shaded area represents 95% confidence interval. Source: Kashiwagi (2014)

ANALYSIS OF THE ESA SECTION 4(A)(1) FACTORS

The ESA requires NMFS to determine whether a species is endangered or threatened because of any of the factors specified in section 4(a)(1) of the ESA. The following provides information on each of these five factors as they relate to the status of the giant and reef manta rays. The likely contribution of each threat to the extinction risk of the species is evaluated, with “significant” defined as increasing the risk to such a degree that it affects the species’ demographics (i.e., abundance, productivity, spatial structure, diversity) either to the point where the species is strongly influenced by stochastic or depensatory processes or is on a trajectory toward this point.

Present or Threatened Destruction, Modification, or Curtailment of Habitat or Range

Due to their association with nearshore habitats, manta rays are at elevated risk for exposure to a variety of contaminants and pollutants, including brevetoxins, heavy metals, polychlorinated biphenyls, and plastics. Many pollutants in the environment have the ability to bioaccumulate in fish species; however, only a few studies have specifically examined the accumulation of heavy metals in the tissues of manta rays (Essumang 2010; Ooi et al. 2015), with findings that are put in relation to human health risks and consumption of manta rays. For example, Essumang (2010) found platinum levels within *M. birostris* samples taken off the coast of Ghana that exceeded UK dietary intake recommendation levels, and Ooi et al. (2015) reported concentrations of lead in *M. alfredi* tissues from Lady Elliot Island, Australia, that exceeded maximum allowable level recommendations for fish consumption per the European Commission and the Codex Alimentarius Commission (WHO/FAO). While consuming manta rays may potentially pose a health risk to humans, there is no information on the lethal concentration limits of these metals or other toxins in manta rays. Additionally, at this time, there is no evidence to suggest that current concentrations of these environmental pollutants are causing detrimental physiological effects to the point where the species may be at an increased risk of extinction.

Plastics within the marine environment may also be a threat to the manta ray species, as the animals may ingest microplastics (through filter-feeding) or become entangled in the debris, potentially contributing to increased mortality rates. Jambeck et al. (2015) found that the Western and Indo-Pacific regions are responsible for the majority of plastic waste (Figure 8). These areas also happen to overlap with some of the largest known aggregations for manta rays. For example, in Thailand, where recent sightings data have identified over 288 giant manta rays (MantaMatcher 2016), mismanaged plastic waste is estimated to be on the order of 1.03 million tonnes annually, with up to 40% of this entering the marine environment (Jambeck et al. 2015). Approximately 1.6 million tonnes of mismanaged plastic waste is being disposed of in Sri Lanka, again with up to 40% entering the marine environment (Jambeck et al. 2015), potentially polluting the habitat used by the nearby Maldives aggregation of manta rays. While the ingestion of plastics is likely to negatively impact the health of the species, the levels of microplastics in manta ray feeding grounds and frequency of ingestion are presently being studied to evaluate the impact on these species (Germanov 2015b; Germanov 2015a).

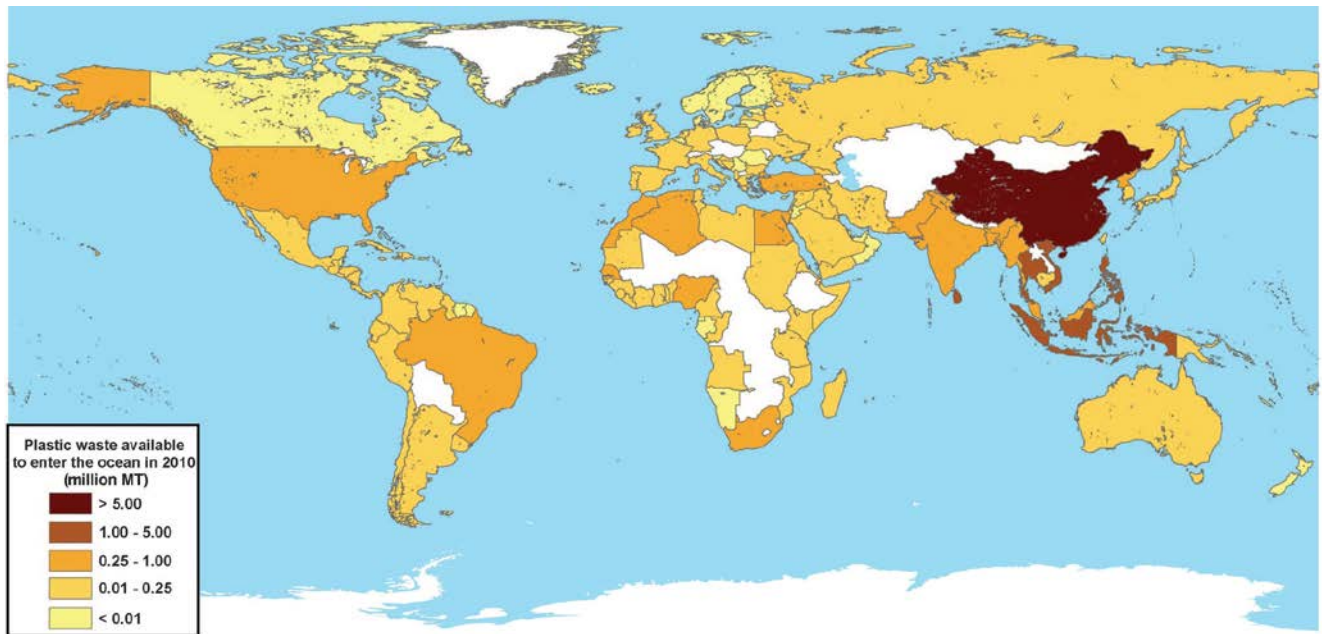


Figure 8. Map representing the estimated amount of mismanaged plastic waste (in millions of metric tons (MT)) by country that was produced in 2010. Countries in white were not included in the analysis. Source: Jambeck et al. (2015).

Because manta rays are migratory and considered ecologically flexible (e.g., low habitat specificity), they may be less vulnerable to the impacts of climate change compared to other sharks and rays (Chin et al. 2010). However, as manta rays frequently rely on coral reef habitat for important life history functions (e.g., feeding, cleaning) and depend on planktonic food resources for nourishment, both of which are highly sensitive to environmental changes (Brainard et al. 2011; Guinder and Molinero 2013), climate change is likely to have an impact on the distribution and behavior of both *M. birostris* and *M. alfredi*.

Coral reef degradation from anthropogenic causes, particularly climate change, is projected to increase through the future. Specifically, annual, globally averaged surface ocean temperatures are projected to increase by approximately 0.7 °C by 2030 and 1.4 °C by 2060 compared to the 1986-2005 average (IPCC 2013), with the latest climate models predicting annual coral bleaching for almost all reefs by 2050 (Heron et al. 2016). As declines in coral cover have been shown to result in changes in coral reef fish communities (Jones et al. 2004; Graham et al. 2008), the projected increase in coral habitat degradation may potentially lead to a decrease in the abundance of manta ray cleaning fish (e.g., *Labroides* spp., *Thalassoma* spp., and *Chaetodon* spp.) and an overall reduction in the number of cleaning stations available to manta rays within these habitats. Decreased access to cleaning stations may negatively impact the fitness of the mantas by hindering their ability to reduce parasitic loads and dead tissue, which could lead to increases in diseases and declines in reproductive fitness and survival rates.

Changes in climate and oceanographic conditions, such as acidification, are also known to affect zooplankton structure (size, composition, diversity), phenology, and distribution (Guinder and Molinero 2013). As such, the migration paths and locations of both resident and seasonal aggregations of manta rays, which depend on these animals for food, may similarly be altered (Australian Government 2012; Couturier et al. 2012). It is likely that those *M. alfredi* populations that exhibit site-fidelity behavior will be most affected by these changes. For example, resident manta ray populations may be forced to travel farther to find available food or randomly search for new productive areas (Australian Government 2012; Couturier et al. 2012). As research to understand the exact impacts of climate change

on marine phytoplankton and zooplankton communities is still ongoing, the severity of this threat to both species of manta rays has yet to be fully determined.

Overutilization for Commercial, Recreational, Scientific, or Educational Purposes

Manta rays are both targeted and caught as bycatch in fisheries worldwide. In fact, according to Lawson et al. (2016), manta ray catches have been recorded in at least 30 large and small-scale fisheries covering 25 countries. The majority of fisheries that target mobulids are artisanal (Croll et al. 2015), with mobulids traditionally targeted for their meat; however, since the 1990s, a market for mobulid gill rakers has significantly expanded, increasing the demand for manta ray products, particularly in China. The gill rakers of mobulids are used in Asian medicine and are thought to have healing properties, from curing chicken pox to cancer, with claims that they also boost the immune system, purify the body, enhance blood circulation, remedy throat and skin ailments, cure male kidney issues, and help with fertility problems (Heinrichs et al. 2011). The use of gill rakers as a remedy, which was widespread in Southern China many years ago, has recently gained renewed popularity over the past decade as traders have increased efforts to market its healing and immune boosting properties directly to consumers (Heinrichs et al. 2011). As a result, demand has significantly increased, incentivizing fishermen who once avoided capture of manta rays to directly target these species (Heinrichs et al. 2011; CITES 2013). According to Heinrichs et al. (2011), it is primarily the older population in Southern China as well as Macau, Singapore, and Hong Kong, who ascribes to the belief of the healing properties of the gill rakers; however, the gill rakers are not considered “traditional” or “prestigious” items (*i.e.*, shark fins) and many consumers and sellers are not even aware that gill rakers come from manta or mobula rays (devil rays). Meat, cartilage, and skin of manta rays are also utilized, but valued at significantly less than the gill rakers, and usually enter local trade or are kept for domestic consumption (Heinrichs et al. 2011; CITES 2013). It is estimated that the value of the manta ray market is around \$5 million per year (S. Heinrichs pers. comm cited in O’Malley et al. (2013)). Based on market surveys conducted in China in Sheung Wan (Hong Kong), Yide Lu (Guangzhou), and Qingping (Guangzhou),

manta gill plate prices ranged from \$166.56 (USD) to \$219.25 (USD) per 500 grams (Hau et al. 2016).

Indonesia, Sri Lanka, and India presently represent the largest manta ray exporting range state countries; however, Chinese gill plate vendors have also reported receiving mobulid gill plates from other regions as well, including Malaysia, China, Taiwan, Vietnam, South Africa, Thailand, Australia, Philippines, Mexico, South America (e.g., Brazil), the Middle East, and the South China Sea (CMS 2014; Hau et al. 2016; O'Malley et al. 2017). Hong Kong, Guangzhou, Singapore, Taiwan, and Macau are the largest importers of manta ray gill plates in Asia (Hau et al. 2016). In 2011, Guangzhou was identified as the main trade center for gill plates (responsible for 99.5% of the estimated total annual market volume), and between 2011 and 2013, the total estimated market volume in Guangzhou had doubled, from 60.15 t to 120.45 t (O'Malley et al. 2017). Based on a conversion of dried gills to estimated number of mobulids, *Manta* spp. comprised 4% (or 4,762 individuals) of the total estimated number of mobulids (n = 130,614) represented in the Guangzhou annual sales (O'Malley et al. 2017). By 2015, Guangzhou saw a significant drop in their market (with estimated total gill plate stocks down to 55% of 2011 levels) (O'Malley et al. 2017). In contrast, the Hong Kong market saw a significant increase in gill plate sales between 2011 and 2015 (from 125 kg to 3,500 kg) (O'Malley et al. 2017), emerging as a new key market for the trade (Hau et al. 2016).

To examine the impact of this growing demand for gill rakers on manta ray populations, information on landings and trends (broken out by species where available) are evaluated for both fisheries that target mantas and those that catch mantas as bycatch.

Targeted Fisheries

Manta rays are reportedly targeted in fisheries in Indonesia, Philippines, India, Thailand, Mozambique, Tonga, Micronesia, Peru, Ghana, and previously in Mexico and possibly the Republic of Maldives. Information on these fisheries is provided below.

Indonesia

Indonesia is reported to be one of the top countries that catch mobulid rays (Heinrichs et al. 2011). Manta and devil ray fisheries span the majority of the Indonesian archipelago, with most landing sites along the Indian Ocean coast of East and West Nusa Tenggara and Java (**Figure 9**) (Lewis et al. 2015).



Figure 9. Map of Indonesia showing identified landing sites of mobulids (represented by black circles, white circles, and red stars). Source: Lewis et al. (2015)

Manta rays (presumably *M. birostris*, but identification prior to the split of the genus) have traditionally been harvested in Indonesia using harpoons and boats powered by paddles or sails, with manta fishing season lasting from May through October. Whereas historically the harvested manta rays would be utilized by the village, the advent of the international gill raker market in the 1970s prompted the commercial trade of manta ray products, with gill plates generally sent to Bali, Surabaya (East Java), Ujung Pandang (Sulawesi), or Jakarta (West Java) for export to Hong Kong, Taiwan, Singapore and other places in Asia (Dewar 2002; White et al. 2006; Marshall and Conradie 2014). This economic incentive, coupled with emerging technological advances (e.g., motorized vessels) and an increase in the number of boats in the fishery, greatly increased fishing pressure and harvest of manta

rays in the 1990s and 2000s (Dewar 2002). In Lamakera, Indonesia, one of the main landing sites for mobulids, and particularly manta rays, Dewar (2002) estimates that the total average harvest of “mantas” during the 2002 fishing season was 1,500 (range 1,050-2,400), a significant increase from the estimated historical levels of around 200-300 mantas per season; however, Lewis et al. (2015) note that this estimate likely represents all mobulid rays, not just mantas. Fishermen from Lamalera, whose fishing grounds overlap with the Lamakera fishing fleet, reported landings of around 200-300 per season but noted that very few mantas were caught from 1998-2001, and attributed the low catch to the presence and competition of Taiwanese fishing ships, which also began fishing off Lamalera in large numbers in the 1990s (Barnes 2005).

Given these amounts, it is perhaps unsurprising that anecdotal reports from fishermen indicate possible local population declines, with fishermen noting that they have to travel farther to fishing grounds as mantas are no longer present closer to the village (Dewar 2002; Lewis et al. 2015). In fact, using the records from Dewar (2002) and community (local) catch records, Lewis et al. (2015) show that there has been a steady decline in manta landings at Lamakera since 2002 (despite relatively unchanged fishing effort), with estimated landings in 2013-2014 comprising only 25% of the estimated numbers from 2002-2006 (**Figure 10**).

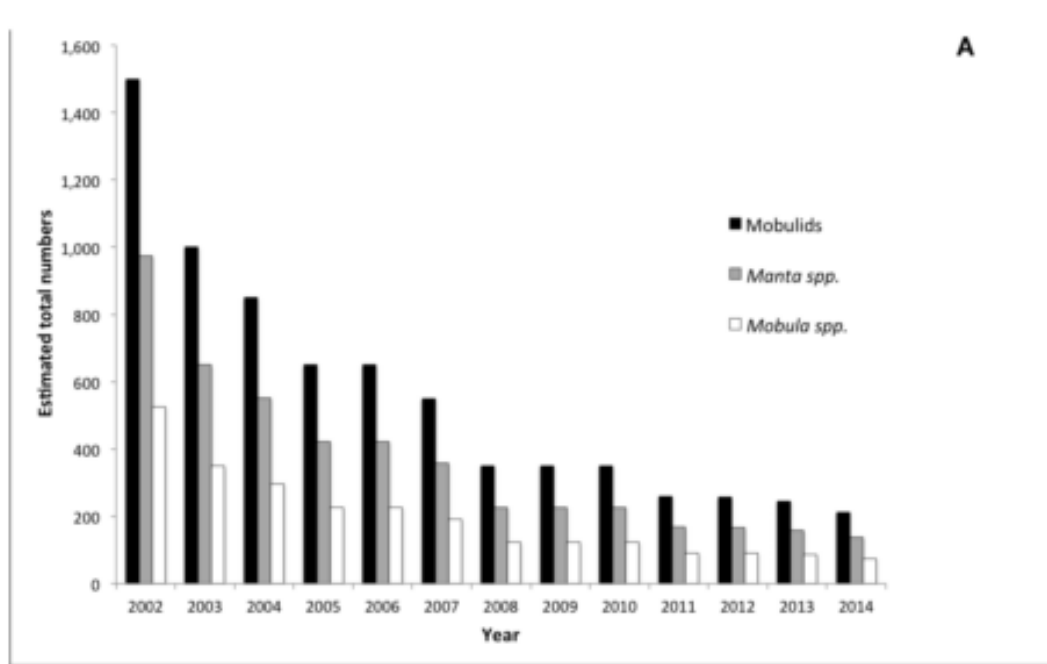


Figure 10. Estimated mobulid landings from Lamakera, Indonesia. Data from 2014 are actual recorded landings by genus. Source: Lewis et al. (2015)

These declines in manta landings are not just limited to Lamakera, but also appear to be the trend throughout Indonesia at the common mobulid landing sites (see **Figure 9** – red star locations). In Tanjung Luar, Lewis et al. (2015) reported a 95% decline in the number of manta landings between 2001-2005 and 2013-2014 (from 272 annual individuals to only 14), with a decrease in the average size of mantas being caught (**Figure 11**). Although effort varied over the time period, the authors suggest that the evidence of substantial decline over periods of both increasing and decreasing effort, as well as decreased size of mantas, strongly indicates an overall decline in the abundance of the species.

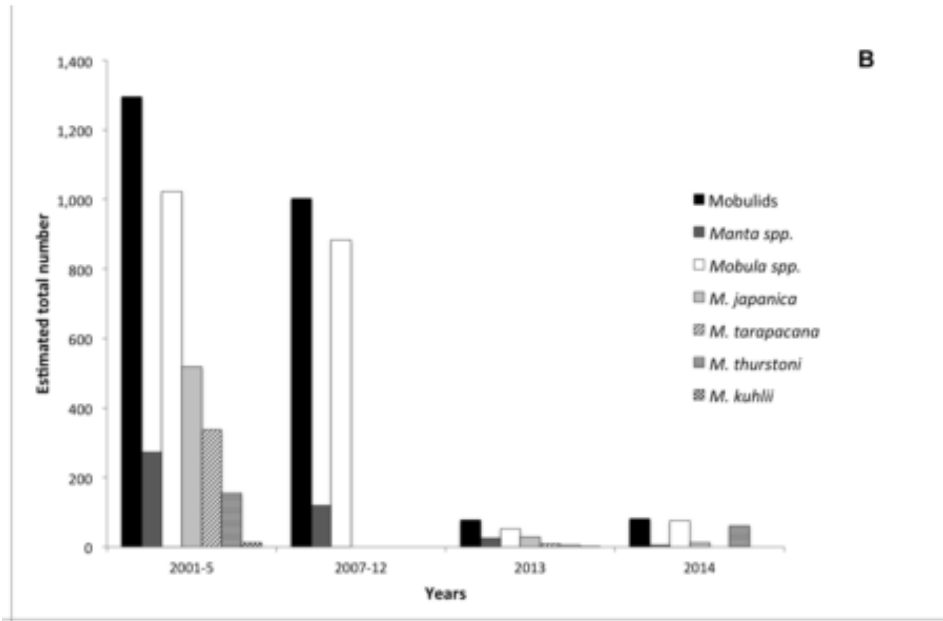


Figure 11. Estimated mobulid landings from Tanjung Luar, Indonesia. Source: Lewis et al. (2015)

In the Cilacap gillnet fishery, where mantas are caught as bycatch during tuna gillnet fishing, the decrease in landings was on the order of 71% between 2001-2005 and 2014 (from an average of 53 mantas per year down to 15) (**Figure 12**) (Lewis et al. 2015).

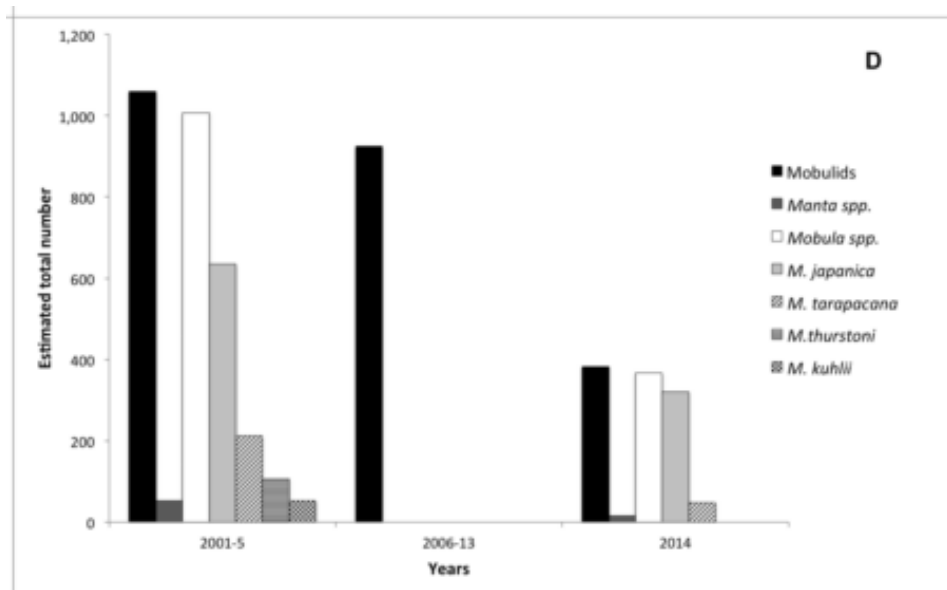


Figure 12. Estimated mobulid landings in gillnet fishery from Cilacap, Indonesia. Source: Lewis et al. (2015).

Areas in Indonesia where manta rays have potentially been fished to extirpation, based on anecdotal reports (e.g., diver sightings data and fishermen interviews), include Lembeh Strait in northeast Sulawesi (after trap nets were installed in the Lembeh Strait channel), Selayer Islands in South Sulawesi, and off the west coast of Alor Island, which may have been an *M. alfredi* population that disappeared within 5 years after a local village installed drift nets in the middle of the channel separating Alor and Pantar Islands (Lewis et al. 2015). Local fishermen who fish in Pulau Banyak off the west coast of Sumatra and catch mantas as bycatch in gillnets have also reported a significant decrease in sightings, possibly a result of bycatch fishing pressure (Lewis et al. 2015).

Although fishing for manta rays was banned within the Indonesian exclusive economic zone (EEZ) in February 2014 (see ***Inadequacy of Existing Regulatory Measures***), in May 2014, manta rays were still being caught and processed at Lamakera, with *M. birostris* the most commonly targeted species (Marshall and Conradie 2014). Around 200 fishing vessels targeting mantas are in operation; however no more than 100 go out at one time, with usually between 30 and 60 per day (Marshall and Conradie 2014). Most of the fishing occurs in the Solor Sea and occasionally in the Lamakera Strait, with landings generally comprising around one to two dozen manta rays per day. Taking into account the manta ray fishing season in Lamakera (June to October), Marshall and Conradie (2014) estimate that between 625 and 3,125 manta rays (likely majority *M. birostris*) may be landed each season. Lewis et al. (2015), however, report a much smaller number, with 149 estimated as landed in 2014.

It is unlikely that fishing effort and associated utilization of the species will significantly decrease in the foreseeable future as interviews with fishermen indicate that many are excited for the new prohibition on manta rays in Indonesian waters because it is expected to drive up the price of manta ray products, significantly increasing the current income of current resident fishermen (Marshall and Conradie 2014). Based on unpublished data, O'Malley et al. (2013) estimates that the total annual income from the manta ray fisheries in Indonesia is around \$442,000 (with 94% attributed to the gill plate trade). Dharmadi et al. (2015) noted that there are still many fishermen, particularly in Raja Ampat, Bali, and Komodo, whose livelihood depends on shark and ray fishing. Without an alternative for

income, it is unlikely that these fishing villages will stop their traditional fishing practices. Additionally, enforcement of existing laws appears to be lacking in this region, with Marshall and Conradie (2014) also observing the practice of blast fishing in the waters surrounding Lamakera, despite this practice being illegal in Indonesian waters. The high market prices for manta products (see **Table 7**) drives the incentive to continue fishing the species, and evidence of continued targeted fishing despite prohibitions suggests that overutilization of the Indonesian manta ray populations is likely to continue to occur into the foreseeable future.

Table 7. Market prices (in rupees (Rp) and U.S. dollars) for mobulid products in Indonesia in A) Tanjung Luar and B) Lamakera. *Estimated for manta ~5m DW. Source: Lewis et al. (2015)

A) Tanjung Luar

	2005 (Aug)	2010 (Jul)	2014 (Jan)	2015 (Jun)
Whole <i>Manta</i> *	1.67 mill. Rp	4.1 mill. Rp		3-6 mill. Rp*
	\$169	\$453		\$225 - \$450
Whole <i>Mobula</i>		1.67 mill. Rp		500K-3 mill. Rp
		\$184		\$38 - \$225
Dried gills / kg - <i>Manta</i> (~ 3-6kg per manta)	275K Rp	800K Rp	2 mill. Rp	1.2 mill. Rp
	\$28	\$88	\$169	\$90
Dried gills /kg - <i>Mobula</i> (~ .5-3kg per mobula)	137.5K Rp			500,000Rp
	\$14			\$38
Mobulid meat / kg (~ 10-50kg per mobuild)	3K Rp	8K Rp	8K Rp	10K Rp
	\$0.30	\$0.88	\$0.68	\$0.75
Skin / cartilage - per <i>Manta</i>	330K Rp			
	\$33			

B) Lamakera

	2002 (May)	2011 (Jul)	2014 (Jan)	2015 (Jun)
Whole <i>Manta</i> *		2 mill. Rp	1 mill. Rp	
		\$234	\$84	
Dried gills / kg - <i>Manta</i>	280K Rp	1 mill. Rp	1.5 mill. Rp	1 mill. Rp
	\$30	\$117	\$127	\$75
Dried gills /kg - <i>Mobula</i>		250K Rp		400K Rp
		\$29		\$30
Mobulid meat / kg	1.5K Rp	6K Rp	6K Rp	6K Rp
	\$0.16	\$0.70	\$0.51	\$0.45
Skin / cartilage - per <i>Manta</i>	60K Rp			
	\$6			

Philippines

In the Philippines, fishing for manta rays mainly occurs in the Bohol Sea and dates back to at least the late 19th century. Based on interviews and historical records, manta rays were hunted by fishermen from the villages in Lila, Pamilacan, Jagna, Sagay, Guinsiliban, and Limasawa (see Figure 13), and utilized primarily for their meat (Acebes and Tull 2016). According to Acebes and Tull (2016), the manta ray fishery can be divided into two distinct periods based on technology and fishing effort: 1) 1800s to 1960, when mantas were mainly hunted in small, non-motorized boats using harpoons from March to May and 2) 1970s to 2013 (present), when boats became bigger and motorized and the fishing technique switched to drift gillnets, with the manta hunting season extending from November to June.

In the earlier period, the manta fishing grounds were fairly close to the shore (<5 km), noted along the coasts of southern Bohol, northwestern and southern coasts of Camiguin and eastern coasts of Limasawa. Boats would usually catch around one manta per day, with catches of 5-10 mantas for a fishing village considered a “good day” (Acebes and Tull 2016). Based on interviews with fishermen from Jagna, there were around 30 to 50 manta ray fishing boats in operation in the 1950s catching mature manta rays (mantas described as being 4-7 m DW) (Acebes and Tull 2016). In Limasawa Island, around 10-20 boats hunted adult manta rays (usual manta size was ~5.5 m DW) although villagers noted that

by the 1950s, catching mantas was not a guarantee, with 5 mantas caught over an entire fishing season considered to be “lucky” (Acebes and Tull 2016). As the fishery became more mechanized in the 1970s, transitioning to larger and motorized boats, and as the primary gear changed from harpoons to non-selective driftnets, fishermen were able to access previously unexplored offshore fishing grounds, stay out for longer periods of time, and catch more manta rays (Acebes and Tull 2016). Additionally, it was during this time that the international gill raker market opened up, increasing the value of gill rakers, particularly for manta species. By 1997, there were 22 active mobulid ray fishing sites in the Bohol Sea (Acebes and Tull 2016). In Pamilacan, 18 boats were fishing for mobulids in 1993, increasing to 40 by 1997, and in Jagna, at least 20 boats were engaged in mobulid hunting in the 1990s (Acebes and Tull 2016). Catches from this time period, based on the recollection of fishermen from Pamilacan and Baclayon, Bohol, were around 8 manta rays (for a single boat) in 1995 and 50 manta rays (single boat) in 1996 (Alava et al. 2002). However, it should be noted that the mobulid fishery ended in Lila and Limasawa Island in the late 1980s and in Sagay in 1997, around the time that the whale fishery ended and a local ban in manta ray fishing was imposed (Acebes and Tull 2016).

Despite increases in fishing effort, catches of mantas began to decline, likely due to a decrease in the abundance of the population, prompting fishermen to shift their fishing grounds farther east and north (**Figure 13**). Although a ban on hunting and selling giant manta rays was implemented in the Philippines in 1998 (see *Inadequacy of Existing Regulatory Measures*), this has not seemed to impact the mobulid fishery in any way. In Pamilacan, there were 14 mobulid hunting boats reported to be in operation in 2011 (Acebes and Tull 2016). In the village of Bunga Mar, Bohol, there were 15 boats targeting mobulids in 2012, and out of 324 registered fishermen, over a third were actively engaged in ray fishing (Acebes and Tull 2016). Due to their size, the boats can only catch a maximum of 4 giant manta rays per trip (Acebes and Tull 2016). Acebes and Tull (2016) monitored the numbers of manta rays landed at Bunga Mar over a period of 143 days from April 2010 to December 2011 (during which there were around 16-17 active fishing boats targeting mobulids), and in total, 40 *M. birostris* were caught. In 2013, records from a single village (location not identified) showed over 2,000 mobulids landed from January to May,

of which 2% (n=51 individuals) were *M. birostris* (Verdote and Ponzo 2014). As there is little evidence of enforcement of current prohibitions on manta ray hunting, and no efforts to regulate the mobulid fisheries, it is unlikely that fishing for mantas will decrease in the future, particularly since fishing is the primary source of income for the people of Jagna and Pamilacan and a “way of life,” with mobulid fishing providing the greatest profit (Acebes and Tull 2016). Based on market surveys and interviews between 2010 and 2012, dried manta meat in the Philippines markets was selling for around \$16-\$23 per kg (Acebes and Tull 2016). Dried gill rakers, which are usually sold to middlemen from Cebu who export them to China or Manila, sold for around \$69 per kg for white gills and up to \$115 per kg for dark gills (Acebes and Tull 2016). Based on these figures, an average manta ray of around 3 m DW could likely fetch up to \$808 (Acebes and Tull 2016).

Although there is a lack of baseline population data for the giant manta rays within the Bohol Sea, it is likely that the continued unregulated fishing on the species will only have negative impacts on the population, particularly given the historical fishing pressure on adults, which increases the likelihood of population decline (Smallegange et al. 2016), and evidence indicating the species has already been fished out of areas of the Bohol Sea. Additionally, while these mobulid fisheries are likely a greater threat to *M. birostris*, Acebes and Tull (2016) notes that there is a new mobulid fishery that became fully active in 2002 off Dinagat Island in northern Mindanao and likely targets *M. alfredi*, given their area of operation (i.e., around seamounts between the islands of Homonhon and Dingat Islands). In 2010, there were 4 active fishing boats, with a fishing season that lasts from May to October, supplying manta ray meat to Bohol during the “off-season” (Acebes and Tull 2016).

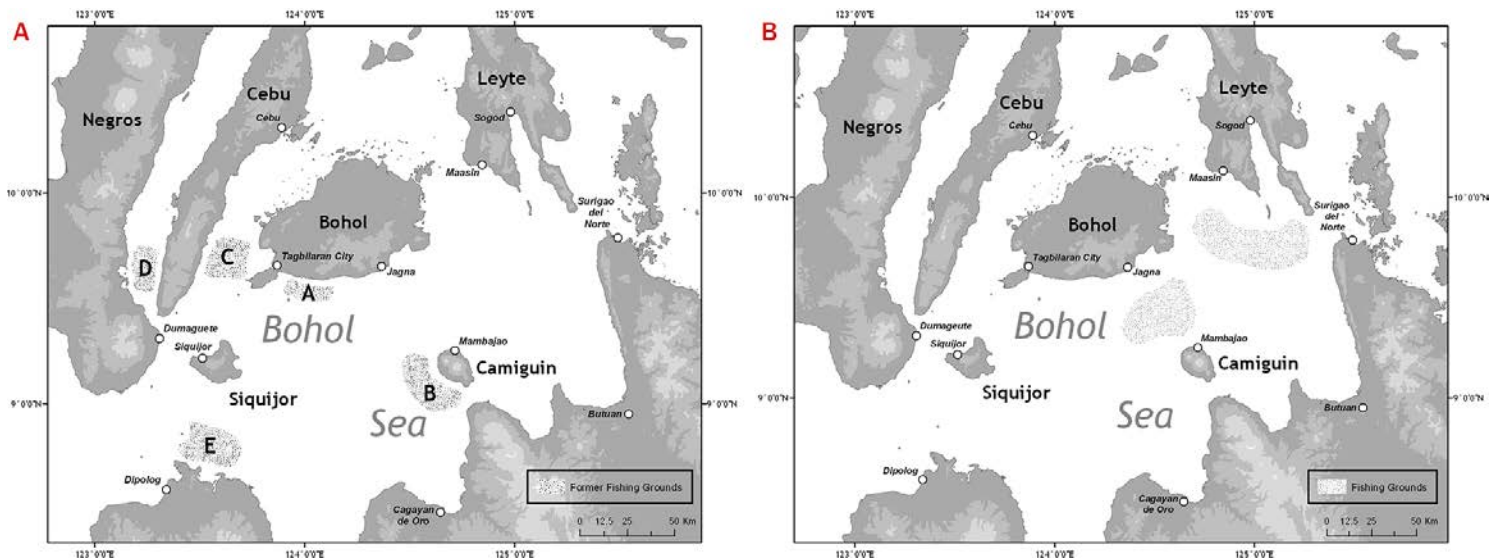


Figure 13. Maps depicting shift in mobulid fishing grounds in the Bohol Sea, Philippines. Mobulid fishing grounds are shaded in light gray. A) Mobulid fishing grounds in 1997; B) Mobulid fishing grounds in recent years. Source: Acebes and Tull (2016)

India

In India, manta rays are mainly landed as bycatch in tuna gillnetting and trawl fisheries. From 2007-2012, landings of mobula rays (including manta rays) on the west coast of India increased significantly from 790 t to 2,694 t, largely due to the targeting of manta and mobula rays for the gill raker market (Nair et al. 2015). Landings specifically of *Manta* spp. (identified primarily as *M. birostris*) increased from 2007 to 2010, with a slight decline in 2011 (Nair et al. 2015). Given the size of these fleets, and limited fisheries oversight, Zacharia et al. (2017) indicate that the actual landing of mobulids are likely significantly underreported. In addition to the gillnet and trawl fisheries, a harpoon fishery at Kalpeni, off Lakshadweep Islands, is also noted for “abundantly” landing mantas (likely *M. alfredi*; A.M. Kitchen-Wheeler pers. comm. 2016) during June – November, with peak season from June-August (Raje et al. 2007). Specific landings figures were unavailable.

Thailand

According to Heinrichs et al. (2011), dive operators in the Similan Islands have observed an increase in fishing for manta rays, including in protected Thai national marine parks, and

between 2006 and 2012, sightings of *Manta spp.* (likely *M. birostris*) had decreased by 76% (CITES 2013b).

Mozambique

In southern Mozambique, within the Inhambane province, reef manta rays are targeted by fishermen, with estimates of around 20-50 individuals taken annually from only a 50 km section of studied coastline (Rohner et al. 2013). As annual estimates of this *M. alfredi* population range only from 149 to 454 individuals (between 2003 and 2007), this take is equivalent to removing anywhere from 4% to 34% of the population per year. This removal rate is potentially unsustainable for a species with such a low productivity, and has likely contributed to the estimated 98% decline that has already been observed in the population (Rohner et al. 2013; Rohner et al. 2017).

Manta birostris has also experienced declines in this area. Whereas previous time-series data, from 2003-2011, showed no clear trend in *M. birostris* sightings (Rohner et al. 2013), expansion of this dataset to include sightings data out to 2016 showed a 94.2% decline in the number of giant manta ray sightings (Rohner et al. 2017b). The authors attribute the decline to a recent and significant increase in the use of large-mesh gillnets off the Inhambane coast; however, landings of manta rays from these fisheries are unquantified, with *M. birostris* rarely observed in the catch (one observed caught over 8-year period) (Rohner et al. 2013; Marine Megafauna Foundation 2016; Rohner et al. 2017b).

Tonga and Micronesia

Opportunistic hunting of manta rays has been reported in Tonga and Micronesia (B. Newton and J. Hartup pers. comms. cited in CMS 2014). While the extent of this fishing and associated impacts on the local manta ray populations (likely *M. alfredi*) are unknown, given the reportedly opportunistic nature of the fishery, it is unlikely that fishing pressure is significant on the species.

Peru

Little information is available on the level of take of manta rays by Peruvian fisheries. Heinrichs et al. (2011), citing to a rapid assessment of the mobulid fisheries in the Tumbes and Piura regions of Peru, reported estimated annual landings of *M. birostris* on the order of 100-220 rays for one family of fishermen. As such, total landings for Peru are likely to be much larger.

Ghana

There is no available data on the amount of manta rays landed in Ghanaian fisheries; however, Debrah et al. (2010) observed that giant manta rays were targeted using wide-mesh drift gillnets in artisanal fisheries between 1995 and 2010. D. Berces (pers. comm. 2016) confirmed that mantas are taken during artisanal fishing for pelagic sharks, and not “infrequently,” with manta rays consumed locally.

Maldives

In the Maldives, Anderson and Hafiz (2002) note that manta rays may be caught in the traditional fisheries, with meat used for bait for shark fishing and skin used for musical drums; however, the authors state that catches are generally very small, potentially as little as 10 t per year.

Mexico

Manta and mobula rays were historically targeted for their meat in the Gulf of California. In 1981, Notarbartolo di Sciara (1988) observed a seasonally-active mobulid fishery located near La Paz, Baja California Sur. Mobulids were fished in the Gulf of California using both gillnets and harpoons, with their meat either fileted for human consumption or used as shark bait. The giant manta ray was characterized as “occasionally captured” by the fishery. While it is unclear how abundant *M. birostris* was in this area, by the early 1990s, Homma et al. (1999) reported that the mobulid fishery had collapsed and CITES (2013), referencing anecdotal dive reports by a filmmaker, noted a decrease in manta ray sightings from 3-4 individuals per dive in 1981 to zero in 1991-1992.

Bycatch

Given the global distribution of manta rays, they are frequently caught as bycatch in a number of commercial and artisanal fisheries worldwide. In a study of elasmobranch bycatch patterns in commercial longline, trawl, purse-seine and gillnet fisheries, Oliver et al. (2015) presented information on species-specific composition of ray bycatch in 55 fisheries worldwide. Based on the available data, Oliver et al. (2015) found that manta rays comprised the greatest proportion of ray bycatch in the purse-seine fisheries operating in the Indian Ocean (specifically *M. birostris*; ~40%) and especially the Eastern Pacific Ocean (identified as *Manta spp.*; ~100%, but would be *M. birostris* as well), but were not large components of the ray bycatch in the longline, trawl, or gillnet fisheries in any of the ocean basins (Figure 14).

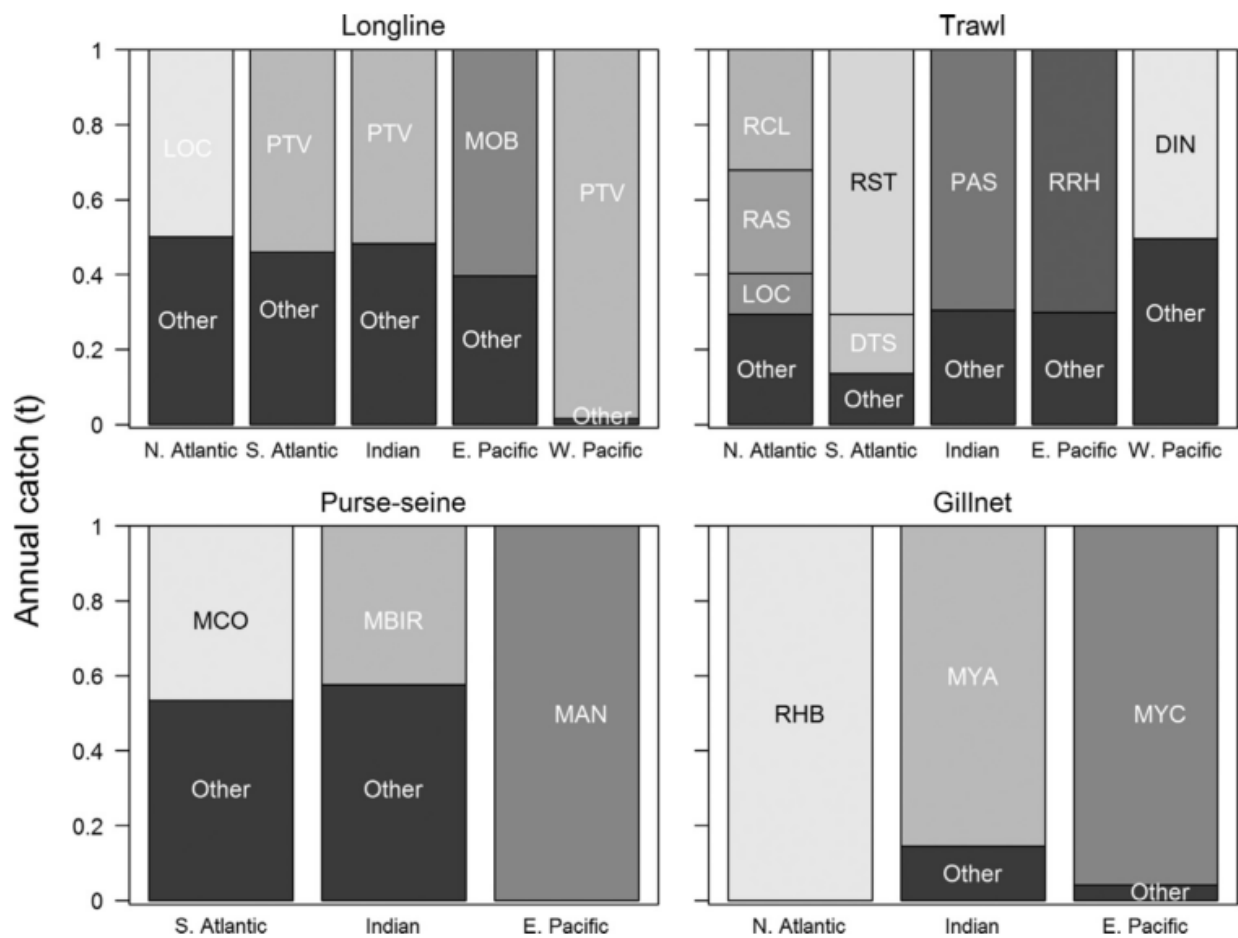


Figure 14. Species composition of ray bycatch by gear type and oceanic region. DIN = *Dipturus innominatus*; DTS = *Dipturus tschudii*; LOC = *Leucoraja ocellata*; MAN = *Manta spp.*;

MBIR = *Manta birostris*; MCO= *Mobula coilloti*; MOB= *Mobula spp.*; MYA = *Myliobatis australis*; MYC = *Myliobatis californica*; PAS = *Pastinachus sephen*; PTV = *Pteroplatyrygon violacea*; RAS = *Raja asterias*; RCL = *Raja clavata*; RHB = *Rhinoptera bonasus*; RRH = *Raja rhina*; RST = *Raja straeleni*. Source: Oliver et al. (2015)

In the Atlantic Ocean, bycatch of giant manta rays has been observed in purse-seine, trawl, and longline fisheries; however, as was noted in the Oliver et al (2015) study, based on the available data, *M. birostris* does not appear to be a significant component of the bycatch.

In the European purse-seine fishery, which primarily operates in the Eastern Atlantic off western Africa, *M. tarapacana* is the predominant mobulid caught as bycatch (Amandè et al. 2010; Hall and Roman 2013). While *M. birostris* is also caught, primarily in Fish Aggregating Device (FAD) purse-seine sets, it does not appear to be caught in large numbers (Amandè et al. 2010; Hall and Roman 2013). Based on data from French and Spanish observer programs, collected over the period of 2003-2007 (27 trips, 598 sets; observer coverage averaged 2.93%), only 11 *M. birostris* were observed caught by the European purse-seine fleet, with an equivalent weight of 2.2 mt (Amandè et al. 2010). Additionally, fishing effort by the Atlantic tuna purse seine fishery is significantly less compared to the effort of the purse-seine fisheries in the other ocean basins, accounting for only 7% of the total number of tuna purse seine sets a year (Croll et al. 2015).

In the U.S. bottom longline and gillnet fisheries operating in the western Atlantic, *M. birostris* is also a rare occurrence in the elasmobranch catch. Based on data from the NMFS shark bottom longline observer program, between 2005 and 2014, only 2 giant manta rays were observed caught by bottom longline vessels fishing in the Gulf of Mexico and South Atlantic, with one discarded alive and one kept (data from 214 observed vessels, 833 trips, and 3,032 hauls; see NMFS Reports available at <http://www.sefsc.noaa.gov/labs/panama/ob/bottomlineobserver.htm>). In the U.S. gillnet fishery, which has been greatly reduced since the implementation of Amendment 2 to the Consolidated Atlantic Highly Migratory Species Fishery Management Plan (NMFS 2007), bycatch of manta rays is low. Based on 1998 – 2015 data from the NMFS Southeast Gillnet Observer Program, which covers all anchored (sink and stab), strike, or drift gillnet fishing by vessels operating in waters from Florida to North Carolina and the Gulf of Mexico, the

number of observed mantas in a given fishing year has ranged from zero to only 16, with the vast majority (around 89%) discarded alive (see NMFS Reports available at <http://www.sefsc.noaa.gov/labs/panama/ob/gillnet.htm>). Since January 2013, no mantas have been observed caught as bycatch.

In Suriname, shrimp trawling, snapper trawling, and snapper longlining take place in depths of up to 80 m, which overlap with the observed depths of *M. birostris* within these waters; however, available information on bycatch of manta rays within these fisheries is largely unavailable (De Boer et al. 2015). In the Atlantic seabob shrimp (*Xiphopenaeus kroyeri*) fishery, where concerns have been raised on the bycatch of chondrichthyan fish, recently installed Turtle Excluder Devices and Bycatch Reduction Devices (which is a square-mesh window panel in the upper side of the codend) appear effective at reducing the bycatch of large pelagic rays, like *M. birostris* (Willems et al. 2013). No other information could be found regarding manta ray bycatch within these waters.

Off Mauritania, Zeeberg et al. (2006) documented *M. birostris* in the bycatch of the European pelagic freezer-trawler fishery. In fact, between October 2001 and May 2005, 9% of the retained pelagic megafauna bycatch (including sharks, bill fish, rays, and cetaceans) from over 1,400 freezer-trawl sets consisted of giant manta rays (Zeeberg et al. 2006). The authors note that the probability of catching manta rays in this region is minimal during the winter and spring (December to June) due to colder water temperatures (around 18°C), but increases as the trade winds decrease towards the end of spring. Based on observer data from July to November (2001-2005), Zeeberg et al. (2006) estimated that between 120 and 620 mature manta rays were removed annually in the Mauritanian EEZ by trawler fisheries, a level the authors concluded was likely unsustainable for the *M. birostris* population. However, as a result of an agreement between the European Union (EU) and Mauritania, which set technical conditions that, according to the Pelagic Freezer-trawler Association (PFA), made commercial fishing economically unviable, the European freezer-trawler fleets have rarely operated in Mauritanian waters since 2012 (PFA 2016).

Overall, given the present low fishing pressure on giant manta rays, and evidence of minimal bycatch of the species, it is unlikely that overutilization as a result of bycatch mortality is a significant threat to the species in the Atlantic Ocean. However, information is severely lacking on both population sizes and distribution of *M. birostris* in the Atlantic and current catch and fishing effort on the species throughout this portion of its range.

In the Indian Ocean, manta rays (primarily *M. birostris*) are mainly caught as bycatch in purse-seine and gillnet fisheries. In the pelagic tuna purse-seine fishery, Romanov (2002) estimated mobula and manta ray bycatch from the western Indian Ocean using observer data collected on Soviet purse seine vessels from 1985-1994. Romanov (2002) further extrapolated the observer data across the principal fishing nations operating within the western Indian Ocean (France, Spain, USSR, Japan, and Mauritius). In terms of numbers of individuals, Romanov (2002) estimated that between 253 and 539 mobulas and mantas (lumped together) were taken per year, with bycatch generally increasing over the time period (**Figure 15**). When compared to the total non-tuna bycatch, mantas and mobulas comprised less than 1% of the total per year.

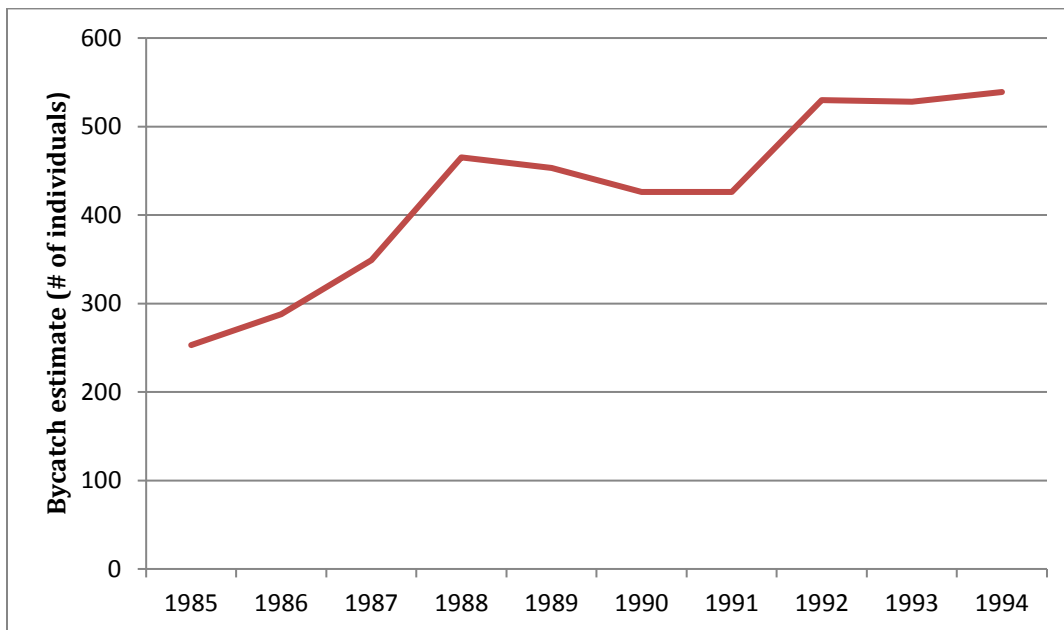


Figure 15. Estimate of bycatch (in numbers) of both manta and mobula rays in the western Indian Ocean by the purse-seine fisheries from 1985-1994. Data source: Romanov (2002)

More recent data suggest that these rays have remained an insignificant portion of the bycatch, indicating that these animals may not be highly susceptible to purse-seine fishery operations in the western Indian Ocean. Both *M. birostris* and *Mobula spp.* are caught in similar amounts, primarily in FAD sets; however, based on 1,958 observed sets from 2003-2007 (coverage rate averaged 4%; **Figure 16**), rays, as a species group, comprised only around 0.7% of the total bycatch. Less than 35 giant manta rays were observed in the bycatch, with around 60% discarded dead and 40% discarded alive (Amandè et al. 2008).



Figure 16. Map showing location of 1,958 observed sets of the European purse seine tuna fishery in the Indian Ocean from 2003-2007. Yellow = Free school sets; Red = FAD sets; Green = seamounts)

Within the Indian Ocean, the available data indicate that manta rays appear to be at higher risk of capture from the fisheries operating in the eastern Indian Ocean, with two of the top three largest *Manta spp.* fishing and exporting range states (Sri Lanka and India) located in this region (Heinrichs et al. 2011).

Sri Lanka

In Sri Lanka, manta rays are primarily caught as bycatch in the artisanal gillnet fisheries. While fishermen note that they generally tend to avoid deploying nets near large aggregations of mantas, or regularly release particularly large mantas (due to the difficulties associated with entanglement and killing the species and loss of boat time), as recently as 2011, manta rays were observed being sold at the Negombo and Mirissa fish markets (Fernando and Stevens 2011).

Negombo is the most popular fish market in the country (Fernando and Stevens 2011). The primary fishing grounds for boats landing at the Negombo market are west and northwest of Sri Lanka, with some venturing as far as the western coast of southern India (Fernando and Stevens 2011). Catches from these boats (serving Negombo) mostly consist of tuna, sharks, billfishes, mobula, and manta rays (Fernando and Stevens 2011). According to Fernando and Stevens (2011), the gill raker dealers at the Negombo market specialize in manta and mobula rays and sell to Asian exporters. The vessels serving the Mirissa fish market tend to fish in the south and southeast of Sri Lanka, sometimes as far as Indonesia, with catches consisting of tuna, billfishes, mobula and manta rays, and some sharks (Fernando and Stevens 2011). However, due to longer at-sea times and unloading practices, the quality of the manta catch is generally lower than that found at the Negombo market (Fernando and Stevens 2011).

While Sri Lankan fishermen state that they try to release pregnant and young manta rays alive, based on 40 observed *M. birostris* being sold at markets (from May through August 2011), 95% were juveniles or immature adults (Fernando and Stevens 2011).

Extrapolating the observed numbers to a yearly value, Fernando and Stevens (2011) estimated annual landings of *M. birostris* at Negombo to be 194 individuals and at Mirissa to be 126 individuals. Using these values, and after making general assumptions about the landings at all of the other fish markets within the country, the authors estimated total annual landings for *M. birostris* in Sri Lanka to be around 1,055 individuals (Fernando and Stevens 2011). While it is difficult to determine whether these levels equate to overutilization of the species within the Indian Ocean, given the lack of baseline population estimates throughout most of the species' range, the authors concluded that the Sri Lankan

fisheries are likely having a “significant and detrimental impact” on the *M. birostris* population that may result in a population crash (Fernando and Stevens 2011).

Additionally, Fernando and Stevens (2011) suggest that the increasing demand for gill rakers in the international market may also influence Sri Lankan fishermen to start keeping all manta rays that are caught as bycatch. However, interviews with fishermen reveal that they do not greatly profit from manta ray fishing; rather, the gill raker dealers and exporters are the ones that see the most economic benefit (Fernando and Stevens 2011). Therefore, while the demand and prices paid for gill rakers have significantly increased in the last 3 to 5 years (Fernando and Stevens 2011), if the economic incentive does not trickle down to the fishermen, it is unlikely that fishing pressure on the species will greatly increase in the foreseeable future. However, that is not to say that the fishing mortality on the species will decrease. Recent data from the IOTC database (<http://www.iotc.org/iotc-online-data-querying-service>) covering the time period of 2012 - 2014 indicate that over 2,400 mt of *M. birostris* were recorded caught by the Sri Lankan gillnet and longline fleets primarily engaged in artisanal fishing. This amount is almost double the 1,413 mt total catch that was reported in Clarke and IOTC Secretariat (2014) by both Sri Lanka and Sudan fleets from a time period that was more than twice as long (2008-2013). Using the maximum observed weight of *M. birostris* in the Indian Ocean (2,000 kg; which was described as “unusually large” (Kunjipalu and Boopendranath 1982)), this translates to a minimum of around 400 giant manta rays caught annually in recent years by Sri Lankan fishing fleets.

India

In India, mobulids are landed as bycatch during tuna gillnetting and trawling operations and are auctioned off for their gill plates, while the meat enters the local markets. Historical reports (from 1961 – 1995) indicate that the species was only sporadically caught by fishermen along the east and west coasts of India, likely due to the fact that the species was rarely found near the shore (Pillai 1998). However, based on available information, it appears that landings have increased in recent years, particularly on the southwest coast. In a snapshot of the Indian tuna gillnet fishery, Nair et al. (2013) provides

evidence of the significant number of mobulids being taken off the coast of Vizhinjam, Kovalam and Colachel, documenting over 1,300 mobulids (50 t) that were landed by fishermen over the course of only 7 days. Of these mobulids, 5 individuals were identified as *M. birostris*. For the years 2003 and 2004, Raje et al. (2007) reported 647 t of *M. birostris* from the southwest coast of India by the trawl fisheries. The significant increase in landings since the mid-1990s is likely due to the demand for the species' gill rakers, with *M. birostris* gill plates characterized as "First Grade" and fetching the highest price at auction at the Cochin Fisheries Harbour (Nair et al. 2013).

While not as abundant on the east coast of India, the species is still occasionally landed as bycatch, primarily in gillnet gear. Raje et al. (2007) documented 43 t of *M. birostris* in 2003 and 2004 and Rajapackiam et al. (2007) reported the landing of 3 mature individuals in 2006 at the Chennai fishing harbor.

Australia

In Australian waters, manta rays (identified as *M. birostris*) were identified as potential bycatch in the Commonwealth Skipjack Tuna Fishery and Western Tuna and Billfish Fishery. However, in a sustainability assessment of these fisheries, Zhou et al. (2009) determined that the current fishing effort poses a low risk to many non-target species caught within this fishery, including manta rays. This is likely due to the minimal spatial overlap between the fishing effort and the species' distribution, with the fraction of distribution area within the fishery area of operation equating to <0.005 for both fisheries (Zhou et al. 2009). Overall, Simpfendorfer (2014) states that there are no data to suggest that *M. alfredi* or *M. birostris* are caught with any frequency or retained in Australian fisheries.

New Zealand

Off New Zealand, manta rays (*M. birostris*) are frequently reported as bycatch in the skipjack tuna (*Katsuwonus pelamis*) purse seine fishery, which operates around the northern North Island (Jones and Francis 2017). Interviews with fishermen indicate that manta ray sightings and encounters peak in January/February as they follow the influx of

warm water (20°) to the area, with manta rays found in around 40-50% of the tuna schools (Jones and Francis 2017). However, the interviewees noted that manta rays are seen as a nuisance, scaring away the tuna from the purse seine net, so when observed in a school, fishermen will generally not target that school (Jones and Francis 2017). Additionally, when caught, fishermen will often attempt to release the manta ray from the net while still in the water (Jones and Francis 2017). As such, they indicate that only rarely are manta rays actually landed on the boat deck (Jones and Francis 2017). In contrast, observer data from 2004/2005 through 2010/2011 indicate that “manta rays” are actually brought on the deck on the boat in a high proportion of these occurrences, which may result in unknown but potentially high levels of post-release mortality (Jones and Francis 2017). However, based on photographic evidence of these occurrences, it is thought that the majority (if not all) of these “manta rays” are actually spinetail devilrays (*Mobula japonica*) and not *Manta birostris* (Jones and Francis 2017).

In the western Pacific fisheries, *Manta* spp. are rarely reported in the bycatch. In the tropical tuna purse seine fisheries, Hall and Roman (2013) note that *M. japonica* represents the most abundant mobulid in the fishery bycatch. Analysis of the catch of Western and Central Pacific Fisheries Commission (WCPFC) purse seine and longline fisheries from 1995-2015 (based on observer data) showed that *M. birostris* is rarely caught (Tremblay-Boyer and Brouwer 2016). In purse seine sets, the species is observed at a rate of 0.0017 individuals per associated set and 0.0076 individuals per unassociated set (Tremblay-Boyer and Brouwer 2016). The available standardized purse seine CPUE data (**Figure 17**) from the Western and Central Pacific Ocean show strong reporting bias trends (as observer reporting in the purse seine fisheries to species-level became more prevalent after 2008), and, therefore, are not particularly useful for accurately assessing abundance trends (Tremblay-Boyer and Brouwer 2016). In the longline fisheries, *M. birostris* is observed at a rate of 0.001-0.003 individuals per 1,000 hooks (Tremblay-Boyer and Brouwer 2016). The longline standardized CPUE data, while short, provides a more accurate representation of the species' abundance trend (due to traditional focus on species in longline observer programs) and indicate that *M. birostris* is observed less frequently in recent years compared to 2000-2005 (**Figure 17**) (Tremblay-Boyer and Brouwer 2016). Based on the

distribution of longline effort from 2000-2015 in the WCPFC longline fisheries, effort has been concentrated around Indonesia and the Philippines (Williams and Terawasi 2016), where significant declines in the species have been observed. Williams and Terawasi (2016) also note that there has been a growth in the domestic fleets operating in the South Pacific over the past decade, with effort clearly increasing between 2004 and 2015.

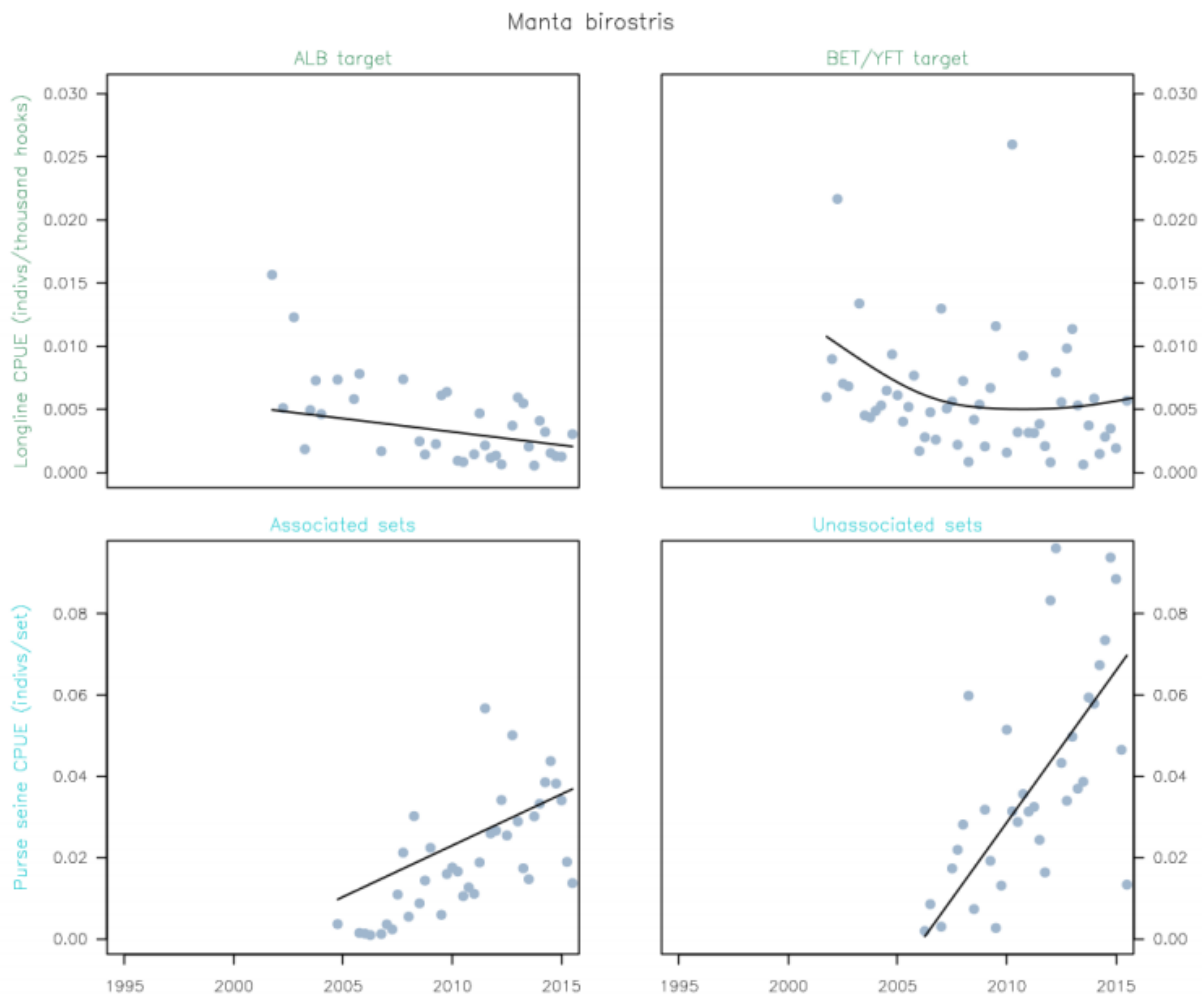


Figure 17. Observed catch per unit effort (CPUE) of *M. birostris* from 1995-2015 in longline sets (albacore (ALB) and bigeyes and yellowfin tuna (BET/YFT) target sets) and purse seine sets (associated and unassociated) within the Western and Central Pacific Ocean, standardized to observed number of individuals per observed hook using 95th percentile. Source: Tremblay-Boyer and Brouwer (2016).

Additionally, a sharp decline in the catches of manta rays off Papua New Guinea, where WCPFC fishing effort is high, was observed in Papua New Guinea purse seiner bycatch in

2005/2006 (C. Rose pers. comm. cited in Marshall et al. 2011b). This occurred after a previously steady rise in manta ray catches from 1994-2005/2006, where manta rays (presumably *M. alfredi*) comprised, on average, 1.8% of the annual bycatch (C. Rose pers. comm. cited in Marshall et al. 2011b).

Overall, given that the majority of observed declines in landings and sightings of manta rays originate from this portion of their range (**Table 5**), additional pressure on these species through bycatch mortality may have significant negative effects on local populations within this region. This is particularly a risk for *M. birostris*, which appears to be the species more frequently observed in the fisheries catch and bycatch, with this pressure already contributing to declines in the species (of up to 95%) throughout many areas (i.e., Indonesia, Philippines, Sri Lanka, Thailand, Madagascar; **Table 5**) within this portion of its range. Given the high market prices for manta ray gill plates, the practice of landing the species as valuable bycatch will likely continue through the foreseeable future.

Manta ray bycatch has also been identified in a few fisheries operating in the South and Central Pacific:

United States

Manta rays have been identified in U.S. bycatch data from fisheries operating primarily in the Central and Western Pacific Ocean, including the U.S. tuna purse seine fisheries, the Hawaii-based deep-set and shallow-set longline fisheries for tuna, and the American Samoa pelagic longline fisheries. However, based on the low estimates of *M. birostris* bycatch in the U.S. tuna purse seine fishery (1.69 mt in 2015) (Secretariat of the Pacific Community, unpublished data, 2016), Hawaii-based deep-set longline fisheries (0.20 mt in 2011; 0.44 mt in 2012; 0.20 mt in 2013) (NMFS 2016b), Hawaii-based shallow-set longline fishery (0.12 mt in 2011)(NMFS 2016b), and American Samoa pelagic longline fisheries (0.44 mt in 2011; 1.16 mt in 2012; 0.32 mt in 2013) (NMFS 2016b), impacts on the giant manta ray are likely to be minimal. Available observer data from these fisheries further support this finding, indicating very low bycatch. The CPUE (individuals per 1,000 hooks) has ranged between <0.001 and 0.003 in the Hawaii deep-set longline fishery since 2002, with approximately 20% observer coverage, between 0 and 0.005 in the Hawaii shallow-set

longline fishery since 2004, with 100% observer coverage, and between <0.001 and 0.003 in the American Samoa longline fishery since 2007, with approximately 20% observer coverage (Western Pacific Regional Fisheries Management Council pers. comm. 2017, citing NMFS Pacific Islands Observer Program unpublished data).

Kirabati

In Kirabati, manta rays (likely *M. alfredi*) are reportedly caught as bycatch in gillnets. According to a local dive operator, the local population has suffered significant declines (O'Malley et al. 2013); however, no data are available and no other information could be found regarding the fishery or the manta ray population.

Overall, there is little evidence of significant fishing pressure on either species throughout the Central or South Pacific.

In the eastern Pacific, giant manta rays are frequently reported as bycatch in the purse seine fisheries; however, identification to species level is difficult, and, as such, most manta and devil ray captures are pooled together (Hall and Roman 2013). According to data provided in Hall and Roman (2013), prior to 2005, catch and bycatch (defined as individuals retained for utilization and individuals discarded dead, respectively) of manta rays in these purse seines remained below 20 t (data from 1998-2004), but by 2005, it was around 30 t and jumped to around 150 t in 2006. In 2008, catch and bycatch had dropped to 40 t and in 2009 decreased further to less than 10 t (Hall and Roman 2013).

Based on reported *M. birostris* catch to the Inter-American Tropical Tuna Commission (IATTC), including available national observer program data, an average of 135 giant manta rays were estimated caught per year from 1993-2015 in the eastern Pacific purse seine fishery by IATTC vessels (**Table 8**) (Hall unpublished data). Bycatch per set ranged from 0.001 individuals (in log associated sets) to 0.027 individuals (in school associated sets) (Hall unpublished data). In 2015, catches of manta and mobula rays by IATTC large purse seine vessels with observers was 71 t (IATTC 2016).

Table 8. Bycatch of giant manta rays and unidentified manta and devil rays (in numbers per set and average numbers per year) in the Eastern Pacific Ocean by the Inter-American Tropical Tuna Commission purse-seine vessels from the time period of 1993-2015.

Species	Time Period	Bycatch per set	Average annual capture (individuals per year)
Giant manta	1993-2015	0.001 – 0.027 (depending on type of set)	135
Unidentified manta/devil ray	1993-2015	0.012-0.221	1,795

While the impact of these bycatch levels on giant manta ray populations is uncertain, effort in the fishery appears to coincide with high productivity areas, such as the Costa Rica Thermal Dome, west of the Galapagos, off the Guayas River estuary (Ecuador), and off central and northern Peru (see **Figure 18**), where giant mantas are likely to aggregate and have been observed caught in sets (Hall and Roman 2013). If effort is concentrated in manta ray aggregation areas, this could lead to substantial declines and potential local extirpations of giant manta ray populations. In fact, a recent preliminary productivity and susceptibility analysis (PSA) indicates that the giant manta ray is one of the most vulnerable species to overfishing in the purse seine fishery by IATTC vessels (Duffy and Griffiths 2017). Specifically, the PSA compared 32 species and calculated vulnerability scores as a combination of the species’ productivity and susceptibility to the fishery (Duffy and Griffiths 2017). Out of the three models run, giant manta rays were always one of the top five most vulnerable species (Duffy and Griffiths 2017).

Already, evidence of declines in this portion of the giant manta ray’s range is apparent, with White et al. (2015) estimating an 89% decline in the relative abundance of *M. birostris* off Cocos Island, Costa Rica. Presently, the largest population of *M. birostris* is thought to reside within the waters of the Machalilla National Park and the Galapagos Marine Reserve (Hearn et al. 2014); however, given the distribution of purse seine fishing effort, and the migratory nature of the species, it is likely that individuals from this population are highly susceptible to being caught by the purse seine fisheries operating in the area.

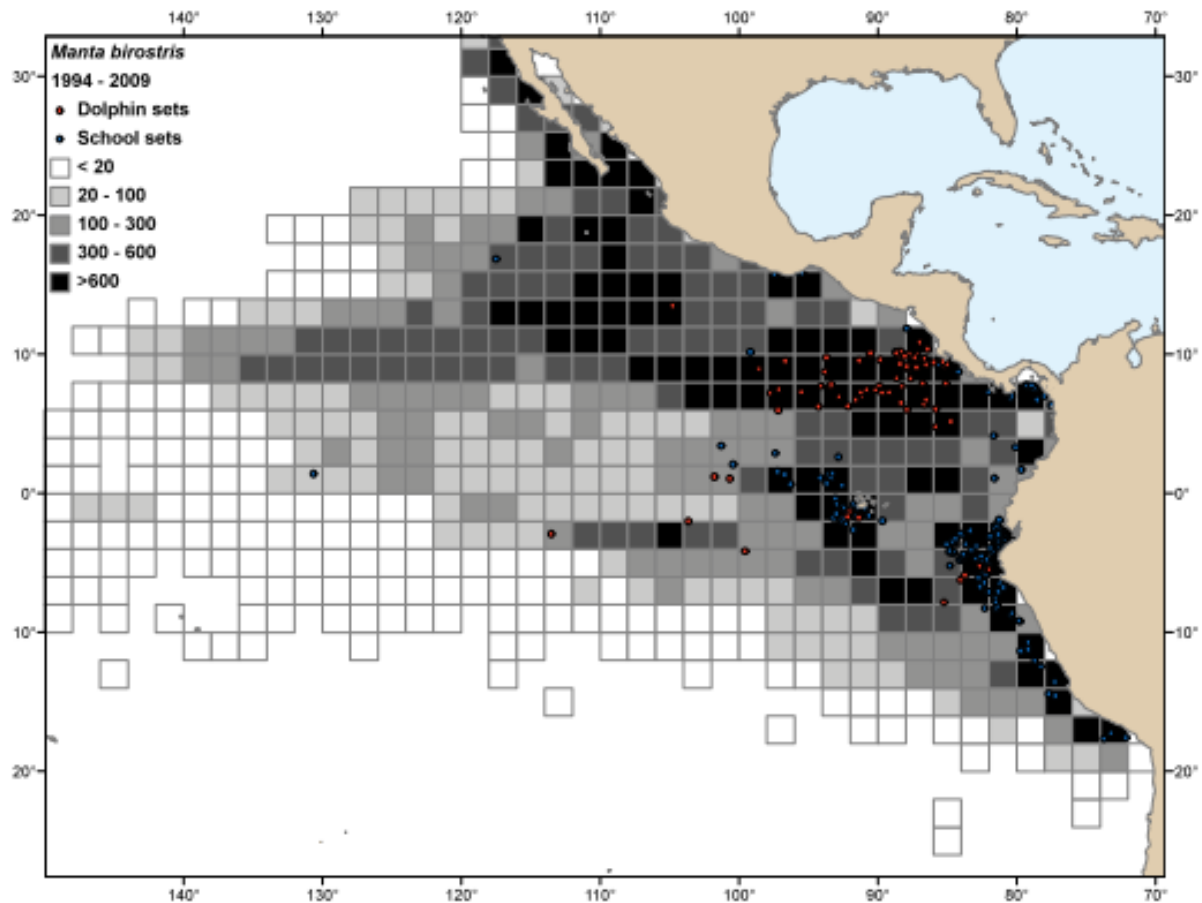


Figure 18. Distribution of purse-seine effort and capture of *M. birostris* in dolphin and school sets in the Eastern Pacific Ocean from 1994-2009. Blue dots = presence of giant manta rays in school sets; Red dots = presence of giant mantas in dolphin sets. Blocks and shading represent effort (i.e., number of sets). Source: Hall and Roman (2013)

Bycatch of manta rays in the eastern Pacific has also been reported from the United States and Peru.

United States

In U.S. west coast fisheries, *M. birostris* is occasionally observed as bycatch in the California drift gillnet fishery targeting swordfish and threshers, but in low numbers and only during El Niño events. In fact, from 1990 – 2006, only 14 giant manta rays were observed caught, with 36% released alive. Estimated (extrapolated) catch for the entire period was 90 individuals (95% CI: 26 – 182; CV = 0.48) (Larese and Coan 2008). Since 2010, no manta

rays have been observed caught in the California drift gillnet fishery (data available from: http://www.westcoast.fisheries.noaa.gov/fisheries/wc_observer_programs/sw_observer_program_info/data_summ_report_sw_observer_fish.html).

Peru

In 2005, interviews with northern Peruvian fishermen indicate that manta rays are rather frequently caught in gillnet gear, with 55% of respondents noting *Manta spp.* as bycatch (Ayala et al. 2008). In 2005, gillnet boats comprised 33% of the total artisanal fishing fleet of Peru (Ayala et al. 2008). However, fishermen off Salaverry and Chimbote did not view manta rays as a commercially viable species. Additionally, Ayala et al. (2008) noted that catching manta rays is actually dangerous for the fishermen operating the smaller artisanal vessels, as the animals tend to cause nets to be lost and can also potentially sink the small boats (Ayala et al. 2008). More recently, between January 2015 and February 2016, Alfaro-Cordova et al. (2017) monitored captures and fish-market landings of manta and devil rays by small-scale gillnet fisheries at three landings sites in northern Peru. The authors found that while mobulid ray catch (particularly immature *Mobula japonica*) was relatively high (mean nominal CPUE = 1.6 ± 2.8 mobulids [km.day]⁻¹ and peak CPUE of 10.17 ± 2.3 mobulids [km.day]⁻¹), no manta rays (*M. birostris*) were observed caught, although one was observed landed (Alfaro-Cordova et al. 2017), suggesting that fishermen may be actively avoiding manta rays. Manta rays have also been reported as bycatch in the Peruvian merluza fishery, which uses mid-water trawls in 50-150 m depths (Stewart et al. 2016b), and in the small-scale Peruvian drift net fishery targeting primarily blue and short fin mako sharks (Alfaro-Shigueto et al. 2010).

Overall, given the sustained fishing pressure on *M. birostris* in the eastern Pacific, particularly its susceptibility to the industrial tuna purse-seine fisheries operating near high productivity areas where the species is likely to aggregate, and evidence of subsequent population declines of up to 88%, it is likely that current fisheries-related mortality rates are a threat significantly contributing to the overutilization of the species in this portion of its range.

Shark Control Programs

In addition to targeted fisheries and bycatch, manta rays may also suffer mortality in nets deployed to control sharks off the coasts of Australia and South Africa. In Australia, shark control nets are deployed off the east coast of Queensland and New South Wales (NSW). Since 2001, 194 manta rays (species not identified) have been observed caught in the Queensland nets, with around 52% released alive (<https://data.qld.gov.au/dataset/shark-control-program-non-target-statistics-by-year>). In New South Wales, only 2 *M. birostris* individuals were caught in 2014 by the shark control nets, both released alive. Prior years (2010-2013) reported no captures of manta rays (annual reports of the NSW Shark Meshing Program).

In South Africa, the KwaZulu-Natal shark control program sets nets off the eastern coast. Catches from this program, adapted from Cliff and Dudley (2011), are provided in **Table 9**.

Table 9. Annual catch (mean) of *Manta* spp. individuals in the KwaZulu-Natal shark control program nets off the coast of South Africa from 1981 – 2009. The percent of the catch released alive is also provided. SD = standard deviation.

Species	Annual catch (1981-1989)			Annual catch (1990-1999)			Annual catch (2000-2009)		
	Mean	SD	% released alive	Mean	SD	% released alive	Mean	SD	% released alive
<i>Manta</i> spp. (likely <i>M. alfredi</i>)	52	32.6	65	70	33.9	67	43	28.8	59

The data from Cliff and Dudley (2011) are broken up into three decades based on differences in reporting and effort over the entire time period. The last decade (2000-2009) saw a significant reduction in effort (i.e., decrease in km of net/ year), with drumlines replacing almost half of the nets at the 17 southernmost beach locations on Hibiscus Coast (Cliff and Dudley 2011). In fact, in these locations, catches of manta rays were significantly reduced, with an average annual catch of <1 between 2007 and 2010 on the drumlines, and a 100% release alive rate (Cliff and Dudley 2011). It is likely that catch

of mantas on shark nets will decrease in the future as efforts to reduce bycatch, such as through a combination of drumlines and nets (with Cliff and Dudley (2011) noting that more nets are planning to be replaced with drumlines for the remaining beaches), continue to be explored into the future.

Disease and Predation

Manta rays are frequently observed congregating in inshore cleaning stations where small cleaner fish remove parasites and dead tissue from their bodies (Marshall and Bennett 2010a; O'Shea et al. 2010; CITES 2013). They may remain at these cleaning stations for large periods of time, sometimes up to 8 hours a day, and may visit daily (Duinkerken 2010; Kitchen-Wheeler 2013; Rohner et al. 2013). These cleaning stations are often associated with inshore coral reefs. While there is no information on manta ray diseases, or data to indicate that disease is contributing to population declines in either species, impacts to these cleaning stations (such as potential loss through habitat degradation) may negatively impact the fitness of the mantas by decreasing their ability to reduce their parasite load.

In terms of predation, manta rays are frequently sighted with non-fatal injuries consistent with shark attacks, although the prevalence of these sightings varies by location (Homma et al. 1999; Ebert 2003; Mourier 2012). Deakos et al. (2011) reported that scars from shark predation, mostly on the posterior part of the body or the wing tip, were evident in 24% of *M. alfredi* individuals (n=70 individuals with injuries) observed at a manta ray aggregation site off Maui, Hawaii. At Lady Elliott Island, off eastern Australia, Couturier et al. (2014) observed 23% of individuals had shark scars. In contrast, in southern Mozambique, between 2003 and 2006, 76.3% (n=283) of the *M. alfredi* identified by Marshall and Bennett (2010a) exhibited shark-inflicted bite marks, the majority of which were already healed. Rohner et al. (2013) found a lower rate for *M. birostris*, with only 35% of individuals observed with bite marks. Marshall and Bennett (2010a) also recorded two mid-pregnancy abortions by pregnant female *M. alfredi* attributed to damage from shark attacks. The authors observed that the rate of shark-inflicted bites in southern Mozambique appears to be higher than predation rates in other manta ray populations,

which is generally noted at <5% (Ito 2000; Kitchen-Wheeler et al. 2012). It is unknown why this difference exists.

In terms of fatal encounters, there are a couple of records of killer whales feeding on manta rays. In Papua New Guinea, Visser and Bonoccorso (2003) observed on two separate occasions orcas fatally attacking and feeding on manta rays. Killer whales were also recorded preying on manta rays in the Galapagos Islands (Fertl et al. 1996).

Because the damage from a shark bite usually occurs in the posterior region of the manta ray, there may be disfigurement leading to difficult clasper insertion during mating or inhibited waste excretion (Clark and Papastamatiou 2008). Given the already low reproductive ability of these species, attacks by sharks or killer whales may pose a threat to the species by further impairing the manta rays' ability to rebuild after depletion. However, at this time, the impact of shark bites on manta ray reproduction is speculative.

Inadequacy of Existing Regulatory Mechanisms

Protections for manta rays are increasing, yet there are still a number of areas where manta rays are targeted or allowed to be landed as bycatch. In fact, only one of the Regional Fishery Management Organizations (RFMOs) has prohibited retention of bycatch of manta rays. Additionally, because both manta species were identified as *M. birostris* prior to 2009, some national protections that were implemented before 2009 are specific only to giant manta rays, despite both species being present in that nation's waters. Below provides an analysis of the adequacy of measures in terms of controlling threats to each species where available data permit. A list of current protections for manta rays can be found in the **Appendix** of this report.

Overutilization of *M. birostris*

Based on the available data, *M. birostris* appears to be most at risk of overutilization in the Indo-Pacific and eastern Pacific portions of its range. Targeted fishing and incidental capture of the species in Indonesia, Philippines, Sri Lanka, and India and throughout the eastern Pacific has led to observed declines in the *M. birostris* populations. Despite national protections for the species, poor enforcement and illegal fishing have essentially rendered

the existing regulatory mechanisms inadequate to achieve their purpose of protecting the giant manta ray from fishing mortality.

In Indonesia, *M. birostris* and *M. alfredi* were provided full protection in the nation's waters in 2014 (4/KEPMEN-KP/2014), with the creation of the world's largest manta ray sanctuary at around 6 million km². Fishing for the species and trade in manta ray parts are banned. Despite this prohibition, fishing for manta rays continues, with evidence of the species being landed and traded in Indonesian markets (AFP 2014; Marshall and Conradie 2014; Dharmadi et al. 2015). As mentioned previously (see ***Overutilization for commercial, recreational, scientific, or educational purposes***), many fishermen throughout Indonesia rely on shark and ray fishing for their livelihoods, and without an alternative source of income, are unlikely to stop their traditional fishing practices, including the targeting of manta rays. Additionally, in interviews with fishermen, many viewed the prohibition as a positive because it would likely drive up the market price of manta ray products (Marshall and Conradie 2014). Given the size of the Indonesian archipelago, and current resources, Dharmadi et al. (2015) note there are many issues with current enforcement of regulations. For example, the collection of data is difficult due to insufficient fisheries officers trained in species identification and the large number of landing sites that need to be monitored (over 1,000). Catch data are also usually not accurately recorded at the smaller landing sites either, with coastal waters heavily fished by artisanal fishermen using non-selective gear (Dharmadi et al. 2015). Given the issues with enforcement and evidence of illegal fishing, existing regulatory mechanisms are inadequate to protect the species from further declines due to overutilization.

In 1998, the Philippines introduced legal protection for manta rays; however, similar to the situation in Indonesia, enforcement of the prohibitions is lacking and illegal fishing of the species is evident. For example, in a random sampling of 11 dried products of sharks and rays confiscated for illegal trading, Asis et al. (2016) found that four of the products could be genetically identified as belonging to *M. birostris*. Dried manta meat and gill rakers were frequently observed in markets between 2010 and 2012, and fishing boats specifically targeting mobulids (including mantas) were identified in a number of local fishing villages

in the Philippines, with landings consisting of *M. birostris* individuals. Fishing for mobulids is a “way of life” and the primary source of income for many fishermen, and with the high prices for manta gill rakers in the Philippine markets, it is unlikely that pressure on the species will decrease. With essentially no efforts to regulate the mobulid fisheries in the Philippines, and a severe lack of enforcement of the current manta ray hunting prohibition, current regulations to protect *M. birostris* from overutilization in the Philippines are inadequate.

In the eastern and central Indian Ocean, very few national protections have been implemented for *M. birostris*. Essentially, fishing for the species and retention of bycatch is allowed except within the Republic of Maldives EEZ and within specific marine parks of Western Australia (**Appendix**). Given the declines observed in the species throughout the Indian Ocean (**Table 5**), and the migratory nature of the animal, with the potential for the species to move in and out of protected areas into active fishing zones (e.g., from the Maldives to Lakshadweep, Sri Lanka – a distance of ~820 km, well within the ability of *M. birostris*), it is likely that existing regulatory measures within this portion of the species’ range are inadequate to protect it from overutilization.

In the eastern Pacific portion of the species’ range, the IATTC recently implemented a prohibition on the retention, transshipment, storage, landing, and sale of all devil and manta (mobula and manta) rays taken in its large-scale fisheries (Resolution C-15-04). This regulation went into force on August 1, 2016. Cooperating members must report mobulid catch data and ensure safe release; however, developing countries were granted an exception for small-scale and artisanal fisheries that catch these species for domestic consumption. Given that *M. birostris* is primarily caught as bycatch in the IATTC purse-seine fisheries, the adequacy of this prohibition in protecting the species from overutilization depends on the post-release survival rate of the species. While injuries from entanglements in fishing gear (e.g., gillnets and longlines) have been noted (Heinrichs et al. 2011), at this time, at-vessel and post-release mortality rates for manta rays in purse seine nets are unknown. For other *Mobula* species, Francis and Jones (2016) provided preliminary evidence that may indicate a potential for significant post-release mortality of

the spinetail devilray (*Mobula japanica*) in purse-seine fisheries; however, the study was based on only 7 observed individuals and, because of this, the authors caution that it is “premature to draw conclusions about survival rates.” In fact, based on observer observations in the New Zealand purse seine fishery, mentioned in Francis and Jones (2016), rays that were caught during sets and released were “usually lively” and swam away from the vessel and judged by the observers as “likely to survive.” Although decreasing purse seine fishing effort in manta ray hotspots would significantly decrease the likelihood of bycatch mortality, without further information on post-release survival rates, it is highly uncertain if the prohibition ban will be adequate in decreasing the mortality of the species.

Additionally, in 2016, prohibitions on the fishing and sale of *M. birostris* and requirement for immediate release of mantas caught as bycatch were implemented in Peru (where manta rays are generally caught as bycatch in trawl and gillnet fisheries). Ecuador banned the fishing, landing and sale of manta rays in its waters back in 2010. Given that the largest population of *M. birostris* is found in the waters between Peru and Ecuador (with the Isla de la Plata population estimated at around 1,500 individuals), these prohibitions should provide some protection to the species from fishing mortality when in these waters. However, illegal fishing still occurs in these waters. For example, in Ecuador’s Machalillia National Park (a major *M. birostris* aggregation site), researchers have observed large numbers of manta rays with life-threatening injuries as a result of incidental capture in illegal wahoo (*Acanthocybium solandri*) trawl and drift gillnet fisheries operating within the park (Heinrichs et al. 2011; Marshall et al. 2011a). Depending on the extent of the activities, illegal fishing could potentially contribute to local declines in the population if not adequately controlled. Additionally, given the migratory nature of the species, national protections may not be adequate to protect the species from overutilization throughout its range, particularly when the species crosses boundary lines where protections no longer exist, as evidenced by the significant decline in *M. birostris* observed in Cocos Island National Park, Costa Rica (White et al. 2015).

Overutilization of *M. alfredi*

Despite a significant overlap in range with *M. birostris* in the Indian and Pacific Oceans, and the more near shore and reef-associated resident behavior, *M. alfredi* is rarely identified in commercial and artisanal fisheries catch. While the prior lumping of all manta rays as *M. birostris* may account for these findings, in certain portions of the species' range, the distribution of *M. alfredi* may not overlap with the areas of fishing operations. For example, in the Philippines, Rambahiniarison et al. (2016) explains that capture of reef manta rays is unusual as the main mobulid fishing ground in the Bohol Sea lies offshore in deeper waters, where the presence of the more coastal *M. alfredi* is unlikely (**Figure 19**). And while *M. alfredi* are known to make night time deep-water dives offshore for foraging, the driftnets deployed by the mobulid fishermen are set at night at maximum depths of 40 m and thus do not likely overlap with the species' distribution (Rambahiniarison et al. 2016). However, Acebes and Tull (2016) did observe a new, active mobulid fishery off Dinagat Island in northern Mindanao that appears to target *M. alfredi* around seamounts in the Leyte Gulf, supplying manta ray products to Bohol during the "off season." In 2015, Rambahiniarison et al. (2016) confirmed the landing of a mature male *M. alfredi* specimen (329 cm DW) in Bunga Mar, Bohol, where previously only *M. birostris* had been recorded over the course of four seasons of monitoring. While it is uncertain whether fishing pressure on *M. alfredi* will increase in the future (given that the majority of effort is presently concentrated outside of their distribution), current regulations in the Philippines only prohibit fishing of *M. birostris*, and, as such, are inadequate to protect the species from potential declines in the future.

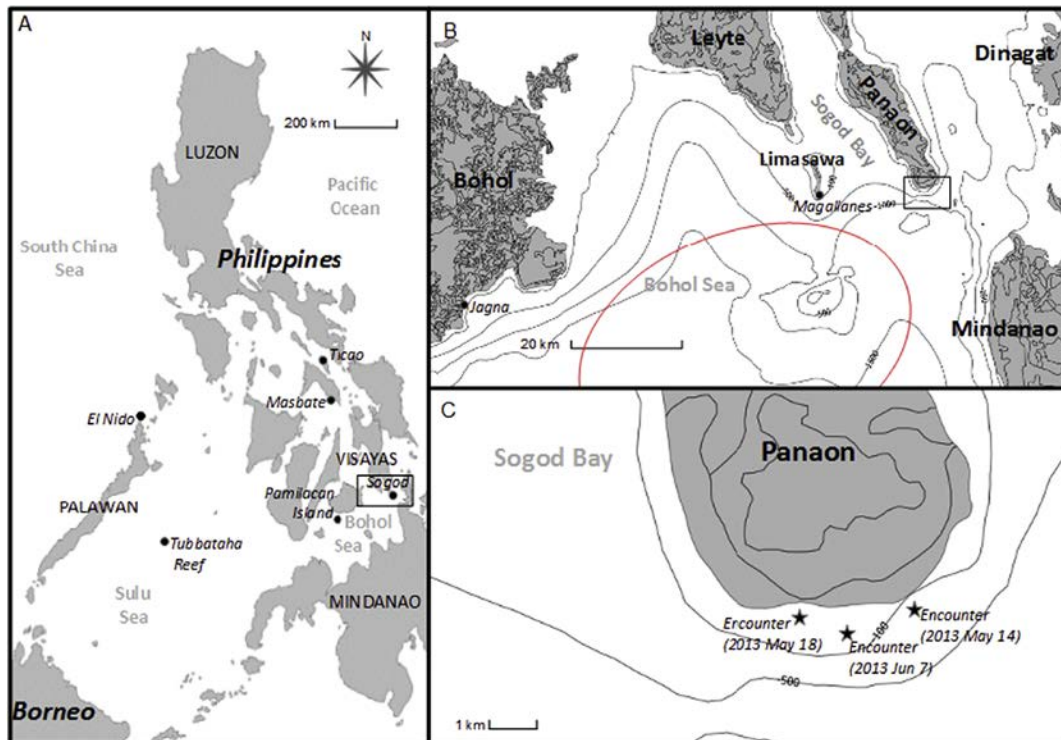


Figure 19. Map showing location of the main mobulid fishing ground in the Bohol Sea, Philippines and observations of *M. alfredi* individuals. A) Map of Philippines; B) Red circle denotes the main area of operation of the offshore driftnet mobulid fishery; C) Stars denote encounters of *M. alfredi*. Source: Rambahinarian et al. (2016)

In Indonesia, while the majority of landings data is reported as *M. birostris*, anecdotal reports from fishermen note that *M. alfredi* used to be caught as bycatch in drift gillnets. Evidence of declines and extirpations of local reef manta ray populations (**Table 5**) suggest that the species is at risk of overutilization by fisheries in these local, inshore areas, despite a lack of records. As such, the inadequacy of existing mechanisms (discussed previously) may pose a threat to the remaining local reef manta ray populations in Indonesia.

In the Indian Ocean, *M. alfredi* is subject to targeted fishing in the western Indian Ocean (off Mozambique) where declines of up to 98% have been observed but no fishery protections or regulatory measures are in place. Whilst the Commonwealth of Australia has now listed both species of Manta on its list of migratory species under its Environment Protection and Biodiversity Conservation Act 1999, which means that any action that may have a significant impact on the species must undergo an environmental assessment and approval

process, there are no specific regulatory protections for the species throughout Western Australian waters. *Manta* spp. are only explicitly protected from targeted fishing within Ningaloo Marine Park and collectively with all species in small designated zones along the Western Australian coast; however, it is important to note that neither species is subject to directed fishing in these waters.

In fact, in portions of the species' range where populations are either not fished and/or are afforded protection and appear stable, existing regulatory measures are adequate in protecting the species from overutilization. These areas include waters of Australia, Hawaii, Guam, Japan, the Republic of Maldives, Palau, and Yap. Given the more coastal and resident behavior of *M. alfredi*, national measures prohibiting fishing of manta rays are likely to provide adequate protection to the species from overutilization through the foreseeable future.

Tourism Impacts

Codes of conduct have been developed by a number of organizations and used by dive operators to promote the safe viewing of manta rays and reduce the potential negative impacts of these activities on manta rays. The Manta Trust, a UK-registered charity, has developed a number of guidelines for divers, snorkelers, tour group operators, and in-water tourists, based on studies of interaction effects conducted by the organization from 2005-2013 (available here: <http://www.mantatrust.org/awareness/resources/>). The Hawaii Association for Marine Education and Research Inc. (2014) notes that codes of conduct for manta ray dive operators have been implemented in a number of popular manta ray diving locales, including Kona, Hawaii, Western Australia, Mozambique, Bora Bora, and in the Maldives; however, information on the adherence to, effectiveness, or adequacy of these codes of conduct in minimizing potential negative impacts of tourism activities on the populations could not be found. In Ecuador, authorities limit daily vessel interaction with mantas off the Isla de la Plata; however, in general, there are very few formal management programs that have been implemented or enforced through government or agency regulatory mechanisms (Venables et al. 2016).

Other Natural or Human Factors Affecting its Continued Existence

Aggregating Behavior

Manta rays are known to aggregate in various locations around the world, in groups usually ranging from 100-1,000 for *M. birostris* and 100-700 for *M. alfredi* (Notarbartolo-di-Sciara and Hillyer 1989; Graham et al. 2012; Venables 2013). These sites function as feeding sites, cleaning stations, or sites where courtship interactions take place (Heinrichs et al. 2011; Graham et al. 2012; Venables 2013). The appearance of mantas in these locations is generally predictable. For example, food availability due to high productivity events tends to play a significant role in feeding site aggregations (Notarbartolo-di-Sciara and Hillyer 1989; Heinrichs et al. 2011; Jaime et al. 2012). Mantas have also been shown to return to a preferred site of feeding or cleaning over extended periods of time (Dewar et al. 2008; Graham et al. 2012; Medeiros et al. 2015). Additionally, mantas exhibit learned behaviors, with diving spots using artificial lights to concentrate plankton and attract manta rays (Clark 2010). For example, a hotel in Hawaii used to operate a manta observation spot, but after it closed in 2004, very low numbers of mantas were observed returning to the spot. However, when the hotel was re-bought and flood lights turned back on, the mantas returned (Clark 2010). Some mantas that used to use the hotel site were sighted at a different feeding area after the closure of the hotel, suggesting that mantas are able to change their home range to accommodate preferred feeding sites. Overall, the predictable nature of their appearances, combined with their slow swimming speeds, large size, and lack of fear towards humans, may increase their vulnerability to other threats, such as overfishing and tourism (discussed below) (O'Malley et al. 2013; CMS 2014).

Impacts of Tourism

Swimming with manta rays is a significant tourist attraction throughout the range of both species. In fact, O'Malley et al. (2013) estimated that the manta ray tourism industry provides \$140 million annually in direct revenue or economic impact (estimated tourist expenditures on dives and associated spending on lodging, food, local transportation) (**Figure 20**). In countries where manta rays are known to be targeted or caught as bycatch, the value of the fishery is substantially less than the estimated value of the tourism industry, suggesting that manta rays are worth significantly more alive than dead. For

example, in Indonesia, O'Malley et al. (2013) estimates that the total annual income from the manta ray fisheries is around \$442,000 (with 94% attributed to the gill plate trade) whereas economic benefits from manta ray tourism is estimated at over \$15 million per year. Globally, O'Malley et al. (2013), citing a personal communication, states that the total trade in manta ray gill plates is around \$5 million per year, less than 4% of the estimated global economic benefit obtained from the tourism industry (\$140 million per year). In fact, the lifetime value of a manta ray for the tourism industry has been estimated to range anywhere from \$100,000 per animal (Anderson et al. 2011b) to \$1.9 million (O'Malley et al. 2013), significantly greater than any value of a manta ray on the market (\$225-\$808) (Lewis et al. 2015; Acebes and Tull 2016).

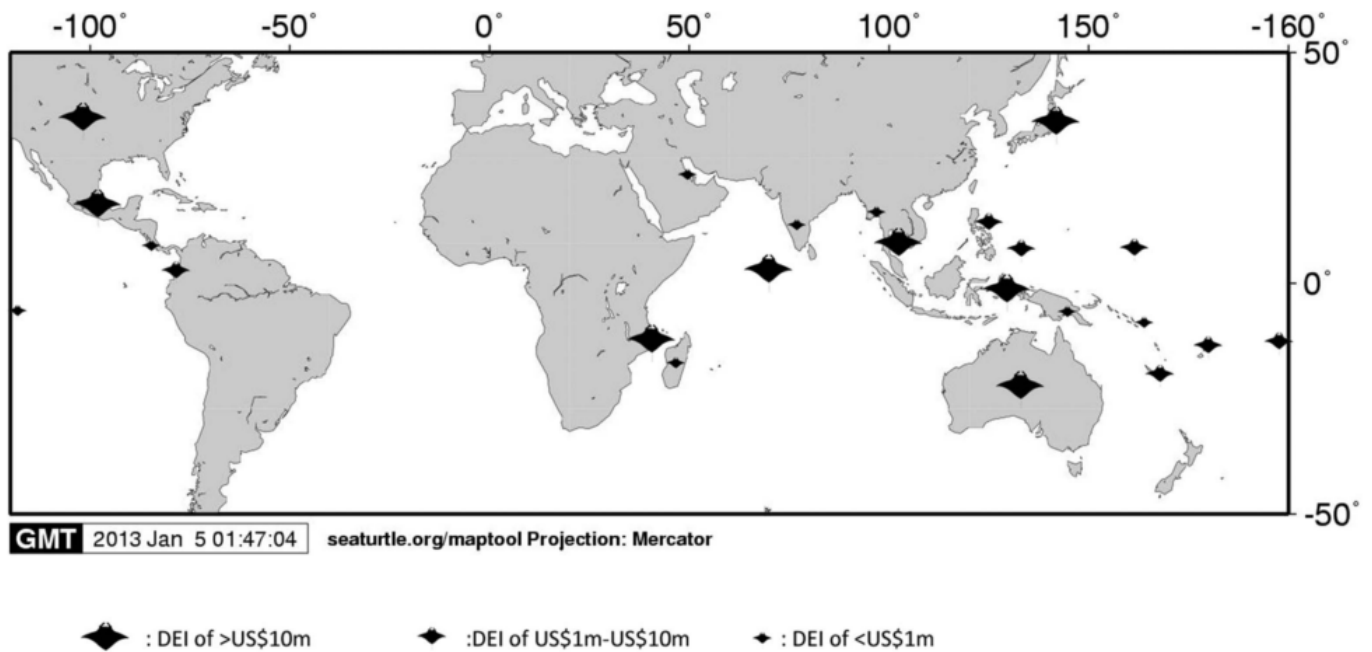


Figure 20. Map showing the direct economic impact (DEI) of manta watching tourism by country. The DEI includes tourist expenditures on manta ray dives and associated costs dives (e.g., food, lodging, transportation). Source: O'Malley et al.

Regular manta ray concentrations off Mozambique, parts of Indonesia, Australia, Philippines, Yap, southern Japan, Hawaii, and Mexico have all become tourist attractions where manta dives are common (Anderson et al. 2011b). Clark (2010) estimates that over 10,000 people per year interact with mantas at Ho'ona Bay in Hawaii. Kashiwagi (2014) notes that Yayemama Islands are one of the world's "top hotspots" for manta ray watching

and supports around 200 dive operations. In the Maldives, which is thought to be home to the largest population of reef manta rays, Anderson et al. (2011b) identified 91 manta ray dive sites and estimated that around 143,000 dives and at least 14,000 snorkeling excursions were conducted annually to view the manta rays from 2006-2008. Five marine protected areas in the Maldives were designated specifically because of the seasonal presence of mantas that create so much tourism revenue, and tourism companies capitalize on this fact with their advertising (Anderson et al. 2011b).

However, while manta ray tourism is far less damaging to the species than the impact of fisheries, this increasing demand to see and dive with the animals has the potential to lead to other unintended consequences that could harm the species. For example, Osada (2010) found that a popular manta dive spot in Kona, Hawaii, had fewer emergent zooplankton and less diversity compared to a less used dive spot, and attributed the difference to potential inadvertent habitat destruction by divers. Tour groups may also be engaging in inappropriate behavior, such as touching the mantas. Given the increasing demand for manta ray tourism, with instances of more than 10 tourism boats present at popular dive sites with over 100 divers in the water at once (Anderson et al. 2011b; Venables 2013), without proper tourism protocols, these activities could have serious consequences for manta ray populations. Already, evidence of tourism activities potentially altering manta ray behavior has been observed. For example, from 2007-2008, low numbers of mantas were observed at normally popular manta dive sites in the Maldives (Anderson et al. 2011b). It is unknown whether this was primarily due to these tourism practices or some change in oceanographic conditions, but manta numbers remained healthy at less visited sites, providing support for the hypothesis that tourism can change their behavior. O'Malley et al. (2013) also reported a dive operator who observed a decrease in manta ray sightings at a notably crowded manta site (location was not specified), indicating tourism may be altering manta ray behavior. Similarly, De Rosemont (2008) noted the disappearance of a resident manta colony from a popular cleaning station in a Bora Bora lagoon in 2005, and attributed the absence to new hotel construction and increased tourism activities; however, by 2007, the author notes that the mantas had returned to the site. In a study of the tourism impacts on *M. alfredi* behavior in Coral Bay, Western

Australia, Venables (2013) observed that mantas exhibited a variety of behavioral changes in response to swim group interactions (i.e., their response was different than their behavior prior to the approach of the swim group). **Figure 21** shows the types of responses that were observed.

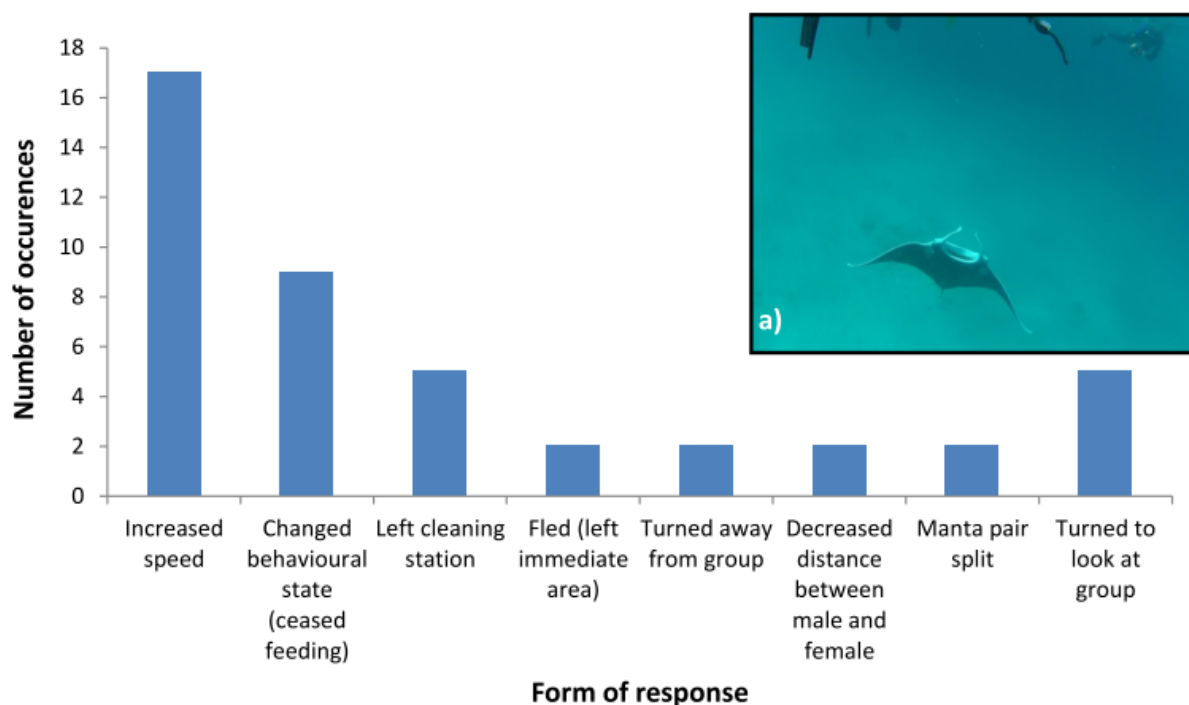


Figure 21. Different behavioral responses of manta rays, and frequency of these responses, to swim group interactions in Coral Bay, Western Australia. Source: Venables (2013)

The tour operators that were observed voluntarily followed a code of conduct for manta ray interactions that was designed to minimize disturbance to the species, and out of the 91 observed swim group interactions, manta rays exhibited a behavioral response in about a third of these interactions (Venables 2013). However, the author notes that out of the 14 manta rays that were specifically observed at a cleaning station, 9 of them left immediately as a response to a tour vessel approaching, a swim group interaction, or an attempt to obtain photo identification, and did not return during the observation period (Venables 2013). Although the long-term effects of tourism interactions are at this time unknown, the results from the Venables (2013) study provide a preliminary estimate of the potentially minimum response of the species to interactions with tourists, and indicates that these

interactions can cause the species to alter (and even stop) behavior that serve critical biological functions (such as feeding and cleaning). Additional studies on both the short-term and long-term impact of tourist interactions with manta rays are needed in order to evaluate if this interaction is a potential threat to the survival of the species.

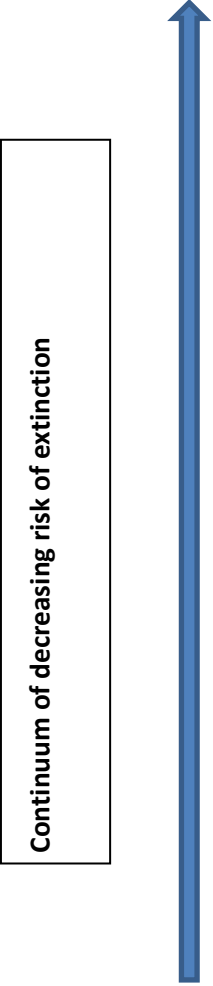
Boat Strikes & Entanglement

Because manta ray aggregation sites are sometimes in areas of high maritime traffic (such as Port Santos in Brazil or in the Caribbean (Marshall et al. 2011a; Graham et al. 2012)), manta rays are at potential risk of being struck and killed by boats. Mooring and boat anchor line entanglement may also wound manta rays or cause them to drown (Deakos et al. 2011; Heinrichs et al. 2011). For example, in a Maui, Hawaii, *M. alfredi* population (n= 290 individuals), Deakos et al. (2011) observed that 1 out of 10 reef manta rays had an amputated or disfigured non-functioning cephalic fin, likely a result of line entanglement. Internet searches also reveal photographs of mantas with injuries consistent with boat strikes and line entanglements, and manta researchers report that such injuries may affect manta fitness in a significant way (The Hawaii Association for Marine Education and Research Inc. 2005; Deakos et al. 2011; Heinrichs et al. 2011; Couturier et al. 2012; CMS 2014; Germanov and Marshall 2014; Braun et al. 2015), potentially similar to the impacts of shark or orca attacks. However, there is very little quantitative information on the frequency of these occurrences and no information on the impact of these injuries on the overall health of the population.

EXTINCTION RISK ANALYSIS

In determining the extinction risk of a species, it is important to consider both the demographic risks facing the species as well as current and potential threats that may affect the species' status. To this end, a demographic analysis was conducted for the giant manta ray and the reef manta ray and considered alongside the information presented on threats to these species in the first section of this status review report. A demographic risk analysis is an assessment of the manifestation of past threats that have contributed to the species' current status and informs the consideration of the biological response of the species to present and future threats. This analysis evaluated the population viability characteristics and trends available for the manta rays, such as abundance, growth rate/productivity, spatial structure and connectivity, and diversity, to determine the potential risks these demographic factors pose to each species. The information from this demographic risk analysis in conjunction with the available information on threats (summarized in a separate threats assessment section below) was interpreted to determine an overall risk of extinction for *M. birostris* and *M. alfredi*. Because species-specific information is sporadic and sometimes uncertain (due to the prior lumping of the Manta genus), qualitative 'reference levels' of extinction risk were used to describe the assessment of extinction risk. The definitions of the qualitative 'reference levels' of extinction risk are provided below:

Qualitative 'Reference Levels' of Extinction Risk

 <p>Continuum of decreasing risk of extinction</p>	<p><u>Low Risk:</u> A species is at low risk of extinction if it is not at moderate or high level of extinction risk (see “Moderate risk” and “High risk” above). A species may be at low risk of extinction if it is not facing threats that result in declining trends in abundance, productivity, spatial structure, or diversity. A species at low risk of extinction is likely to show stable or increasing trends in abundance and productivity with connected, diverse populations.</p> <p><u>Moderate Risk:</u> A species is at moderate risk of extinction if it is on a trajectory that puts it at a high level of extinction risk in the foreseeable future (see description of “High risk” above). A species may be at moderate risk of extinction due to projected threats or declining trends in abundance, productivity, spatial structure, or diversity. *</p> <p><u>High Risk:</u> A species with a high risk of extinction is at or near a level of abundance, productivity, spatial structure, and/or diversity that places its continued persistence in question. The demographics of a species at such a high level of risk may be highly uncertain and strongly influenced by stochastic or compensatory processes. Similarly, a species may be at high risk of extinction if it faces clear and present threats (e.g., confinement to a small geographic area; imminent destruction, modification, or curtailment of its habitat; or disease epidemic) that are likely to create imminent and substantial demographic risks.</p>
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* The appropriate time horizon for evaluating whether a species is more likely than not to be at high risk in the “foreseeable future” depends on various case- and species-specific factors. For example, the time horizon may reflect certain life history characteristics (e.g., long generation time or late age-at-maturity) and may also reflect the time frame or rate

over which identified threats are likely to impact the biological status of the species (e.g., the rate of disease spread). The appropriate time horizon is not limited to the period that status can be quantitatively modeled or predicted within predetermined limits of statistical confidence.

With these caveats in mind, the “foreseeable future” for this extinction risk analysis was considered to extend out several decades (>50 years). Given both species’ life history traits, with longevity estimated to be greater than 20-40 years, maturity ranges from 3 to >15 years, reproductive periodicity anywhere from an annual cycle to a 5-year cycle, with a litter of only 1 pup, and a generation time estimated to be around 25 years, it would likely take more than a few decades (i.e., multiple generations) for any recent management actions to be realized and reflected in population abundance indices. Similarly, the impact of present threats to both species could be realized in the form of noticeable population declines within this time frame, as demonstrated in the very limited available sightings time-series data. As the main potential operative threat to the species is overutilization by commercial and artisanal fisheries, this timeframe would allow for reliable predictions regarding the impact of current levels of fishery-related mortality on the biological status of the species. Additionally, this time frame allows for consideration of the previously discussed impacts on manta ray habitat from climate change and the potential effects on the status of these two species.

Demographic Risk Analysis

Threats to a species’ long-term persistence, such as those evaluated in the **Analysis of the ESA Section 4(A)(1) Factors** section of this review, are manifested demographically as risks to its abundance; productivity; spatial structure and connectivity; and genetic and ecological diversity. These demographic risks thus provide the most direct indices or proxies of extinction risk. In this section, the current status of each of these risks is assessed in turn by responding to a set of questions adapted from McElhany et al. (2000) and incorporated into the NMFS *Guidance on Responding to Petitions and Conducting Status Reviews under the Endangered Species Act* (NMFS 2016a). These questions are based on general conservation biology principles applicable to a wide variety of species. These questions were used as a guide to the types of considerations that are important to each of

the broader demographic risk categories of abundance, productivity, spatial structure, and diversity.

Below provides the discussion of the demographic risks for each species.

Abundance

- *Is the species' abundance so low that it is at risk of extinction due to environmental variation or anthropogenic perturbations (of the patterns and magnitudes observed in the past and expected in the foreseeable future)?*
- *Is the species' abundance so low, or variability in abundance so high, that it is at risk of extinction due to depensatory processes?*
- *Is the species' abundance so low that its genetic diversity is at risk due to inbreeding depression, loss of genetic variants, or fixation of deleterious mutations?*
- *Is the species' abundance so low that it is at risk of extinction due to its inability to provide important ecological functions throughout its lifecycle?*
- *Is the species' abundance so low that it is at risk due to demographic stochasticity?*

M. birostris - Current and accurate abundance estimates are unavailable for the giant manta ray as the species tends to be only sporadically observed. While observations of individuals in local aggregations range from around 40 individuals to over 600, estimates of subpopulation size have only been calculated for Mozambique (n=600) and Isla de la Plata, Ecuador (n=1,500).

If a population is critically small in size, chance variations in the annual number of births and deaths can put the population at added risk of extinction. Demographic stochasticity refers to the variability of annual population change arising from random birth and death events at the individual level. When populations are very small, chance demographic events can have a large impact on the population. The conservation biology "50/500" rule-of-thumb suggests that the effective population size (N_e ; the number of reproducing individuals in a population) in the short term should not be <50 individuals in order to avoid inbreeding depression and demographic stochasticity (Franklin 1980; Harmon and Braude 2010). In the long-term, N_e should not be < 500 in order to decrease the impact of

genetic drift and potential loss of genetic variation that will prevent the population from adapting to environmental changes (Franklin 1980; Harmon and Braude 2010).

Given the two available subpopulation estimates, *M. birostris* is not likely to experience extreme fluctuations that could lead to depensation; however, data are severely lacking. The threshold for depensation in giant manta rays is also unknown. Additionally, the genetic diversity in the giant manta ray has not been investigated. While a preliminary study suggests that the species may exist as isolated subpopulations, available tracking information indicates these manta rays are pelagic and migratory and can likely travel large distances to reproduce. It is this more transient and pelagic nature of the species that has made it difficult to estimate population sizes.

Yet, given the reports of anecdotal declines in sightings and decreases in *M. birostris* landings (of up to 95%) in areas subject to fishing (particularly the Indo-Pacific and eastern Pacific portions of the species' range), with take estimates that currently exceed those subpopulation and aggregation estimates (e.g., 50 – 3,125 individuals), abundance of these particular populations may be at levels that place them at increased risk of genetic drift and potentially at more immediate risks of inbreeding depression and demographic stochasticity. Extirpations of these populations would inherently increase the overall risk of extinction for the entire species.

M. alfredi - Current and accurate abundance estimates are unavailable for the reef manta ray. Observations of individuals in local aggregations range from 35 individuals to over 2,400; however, many are on the order of 100-600 individuals. Subpopulation sizes range from 100 to 350, with the exception of the Maldives at 3,300-9,677 individuals. Meta-population estimates for Southern Mozambique and Ningaloo Reef, Australia are 802-890 and 1,200-1,500 individuals, respectively.

The rather low subpopulation estimates for *M. alfredi* throughout most of its range suggest that the species may be at increased risk of genetic drift and potential loss of genetic variation. Unlike the giant manta ray, *M. alfredi* is thought to be a more resident species, with populations that occur year-round at certain sites. This reproductive isolation further increases the risk of inbreeding depression and potential inability of the population to

respond to environmental variation or anthropogenic perturbations. For example, Kashiwagi (2014) recently estimated the effective population size of the *M. alfredi* population off the Yaeyama Islands to be $N_e = 89$ (450378, 95% CI), indicating that the population is not part of a large gene pool and may be close to a level where viability could be jeopardized in the shorter term. Total population was estimated at 165-202 individuals, indicating long-term viability vulnerability. With most available subpopulation estimates ranging only from 100 to 600 individuals (with the exception of Western Australia, Maldives, and Southern Mozambique), it is likely that these populations similarly have low effective population sizes that may increase their vulnerability to inbreeding depression, the loss of genetic variants, or fixation of deleterious mutations.

Overall, based on the information above, the estimates of small and isolated subpopulations throughout most of the species' range, with the three exceptions off Mozambique, Maldives, and Western Australia, inherently place *M. alfredi* at an increased risk of extinction from environmental variation or anthropogenic perturbations. However, the trend in overall abundance of *M. alfredi* is highly uncertain.

Productivity

- *Is the species' average productivity below replacement and such that it is at risk of satisfying the abundance conditions described above?*
- *Is the species' average productivity below replacement and such that it is unable to exploit requisite habitats/niches/etc. or at risk due to compensatory processes during any life history stage?*
- *Does the species exhibit trends or shifts in demographic or reproductive traits that portend declines in per capita growth rate which pose a risk of satisfying any of the preceding conditions?*

M. birostris - The current net productivity of *M. birostris* is unknown due to the imprecision or lack of available abundance estimates or indices. Fecundity, however, is extremely low, with one pup per litter and a reproductive periodicity of 1-2 years. Using estimates of life history parameters for both giant and reef manta rays, Dulvy et al. (2014)

calculated a median maximum population growth rate to be 0.116 (one of the lowest values compared to other shark and ray species), and estimated productivity (r) to be 0.029.

Ward-Paige et al. (2013) calculated a slightly higher intrinsic rate of population increase for *M. birostris* at $r = 0.042$; however, both these estimates indicate that the giant manta ray has very low productivity and, thus, is extremely susceptible to decreases in its abundance.

Given their large sizes, manta rays are assumed to have a fairly high survival rate after maturity (e.g., low natural predation), with estimated annual survival rates for *M. alfredi* populations supporting this assumption. Based on modeling work on *M. alfredi*, adult survival rate was found to be the most significant factor affecting the viability of the population.

No changes in demographic or reproductive traits or barriers to the exploitation of requisite habitats/niches/etc. have been observed.

M. alfredi - The current net productivity of *M. alfredi* is unknown due to the imprecision or lack of available abundance estimates or indices. Fecundity, however, is extremely low, with one to rarely two pups per litter and a reproductive periodicity of anywhere from 1-5 years. Estimated productivity (r) values range from 0.023 to 0.05, indicating that the reef manta ray has very low productivity and, thus, is extremely susceptible to decreases in its abundance.

Annual survival rate for reef manta rays is fairly high. Estimated survival rates for subpopulations range from 0.95 to 1 off Australia, Hawaii, and Japan. In Mozambique, rates were lower, between 0.6-0.7; however shark attacks are also more common in this area. Based on modeling work, Smallegange et al. (2016) showed that population growth rate was most sensitive to changes in the survival of adults.

No changes in demographic or reproductive traits or barriers to the exploitation of requisite habitats/niches/etc. have been observed.

Spatial Structure

- *Are habitat patches being destroyed faster than they are naturally created such that the species is at risk of extinction due to environmental and anthropogenic perturbations or catastrophic events?*
- *Are natural rates of dispersal among populations, meta-populations, or habitat patches so low that the species is at risk of extinction due to insufficient genetic exchange among populations, or an inability to find or exploit available resource patches?*
- *Is the species at risk of extinction due to the loss of critical source populations, subpopulations, or habitat patches?*

M. birostris – The giant manta ray inhabits tropical, subtropical, and temperate bodies of water and is commonly found offshore, in oceanic waters, and near productive coastlines. It occurs over a broad geographic range and is found in all ocean basins. Most tagging and tracking studies indicate that the home range of individuals is likely large, with the species exhibiting migratory behavior and distances tracked of up to 1,500 km. However, a recent study of the *M. birostris* population found off Pacific Mexico suggests there may be a degree of spatial structuring within the species. At this time, it is unknown whether natural rates of dispersal among populations are too low to prevent sufficient gene flow among populations. Additionally, there is no information to indicate that *M. birostris* is composed of conspicuous source-sink populations or habitat patches.

M. alfredi – The reef manta ray is commonly seen inshore near coral and rocky reefs. The species is associated with warmer waters (>21° C) and productive nearshore habitats (such as island groups). It is considered a more resident species than *M. birostris*. While the species has been tracked undertaking long-distance movements (>700 km), usually to exploit off-shore productive areas, reef manta rays tend to return to known aggregation sites, indicating a degree of site-fidelity. Based on photo-identification surveys of the *M. alfredi* population off Maui, Hawaii, Deakos et al. (2011) suggested that geographic barriers, such as deep channels, may be barriers to movement between neighboring *M. alfredi* populations. Collectively, this information suggests that gene flow is likely limited among populations of *M. alfredi*, particularly those separated by deep ocean expanses.

With the exception of the Yaeyama, Japan population of *M. alfredi*, which Kashiwagi (2014) hypothesized may be a “sink” population but is presently increasing with a population growth rate of 1.02-1.03, there is no information to indicate that *M. alfredi* is composed of conspicuous source-sink populations or habitat patches whose loss may pose a risk of extinction.

Diversity

- *Is the species at risk due to a substantial change or loss of variation in life history traits, population demography, morphology, behavior, or genetic characteristics?*
- *Is the species at risk because natural processes of dispersal and gene flow among populations have been significantly altered?*
- *Is the species at risk because natural processes that cause ecological variation have been significantly altered?*

M. birostris - Rates of dispersal and gene flow are not known to have been altered.

Presently, giant manta rays are wide-ranging inhabitants of offshore, oceanic waters and productive coastline ecosystems and thus are continually exposed to ecological variation at a broad range of spatial and temporal scales. As such, large-scale impacts that affect ocean temperatures, currents, and potentially food chain dynamics, may pose a threat to this species. However, given the migratory behavior of the giant manta ray and tolerance to both tropical and temperate waters, these animals likely have the ability to shift their range or distribution to remain in an environment conducive to their physiological and ecological needs, providing the species with resilience to these effects. At this time, there is no information to suggest that natural processes that cause ecological variation have been significantly altered to the point where *M. birostris* is at risk.

M. alfredi - Given their tendency towards site fidelity, *M. alfredi* likely exist as isolated populations with low rates of dispersal and little gene flow among populations. Currently, there is no information to suggest that natural processes that cause ecological variation have been significantly altered to the point where the species is at risk. Reef manta rays have the ability to shift their distribution to remain in an environment conducive to their physiological and ecological needs, providing the species with resilience to these effects.

For example, in response to changing ecological conditions, like the biannual reversal of monsoon currents, reef manta rays will migrate to the downstream side of atolls, potentially to remain in nutrient-rich waters year-round (Anderson et al. 2011a).

Threats Assessment

According to section 4 of the ESA and NMFS' implementing regulations, the Secretary (of Commerce or the Interior) determines whether a species is threatened or endangered as a result of any of the following five section 4(a)(1) factors: (A) destruction or modification of habitat, (B) overutilization, (C) disease or predation, (D) inadequacy of existing regulatory mechanisms, or (E) other natural or man-made factors. Collectively, the Services simply refer to these factors as "threats." The first part of this status review provides a detailed description and analysis of the likely impact of the above factors on the status of the species. Below, we have summarized the impact of each threat identified in terms of its contribution to the extinction risk of the species using the following qualitative risk definitions:

- Very low or low risk
 - It is unlikely that this threat contributes significantly to the species' extinction risk
- Medium risk
 - This threat contributes significantly to long-term risk of extinction (through the foreseeable future), but does not in itself presently constitute a danger of extinction
- High risk
 - This factor contributes significantly to long-term risk of extinction (through the foreseeable future) and is likely to significantly contribute to short-term risk of extinction

Uncertainty

A confidence rating (CR) was given to the impact of each threat based on the available information. Below are the definitions of the confidence rating scores (adapted from the confidence ratings in Lack et al. (2014)):

- ✦ 0 (no confidence) = No information
- ✦ 1 (low confidence) = Very limited information
- ✦ 2 (medium confidence) = Some reliable information available, but inference and extrapolation required
- ✦ 3 (high confidence) = Reliable information with little to no extrapolation or inference required;

Those threats where little to no information was available on the impact on the status of the species (where CR = 0-1), indicating significant uncertainty regarding the risk to the species, are highlighted in gray.

ESA 4(a)(1) Factor	Identified Threats	Risk to <i>M. birostris</i>	CR	Risk to <i>M. alfredi</i>	CR
	Environmental contaminants/pollutants	Low	0	Low	0
	Plastics (marine debris)	Medium	1	Medium	1
	Climate change	Low	1-2	Low-Medium	1-2
	Targeted Fisheries	Medium	2-3	Low	1-2
	Bycatch	Medium	2-3	Low	1-2
	Shark Control Programs	Low	2-3	Low	2-3
	Disease (Parasite Load)*	Low-Medium	0-1	Low-Medium	0-1
	Shark Attacks*	Low	1	Low	1
	Addressing Overutilization	Medium	2-3	Low	2-3
	Addressing Tourism Impacts	Low-Medium	0-1	Low-Medium	0-1
	Aggregating Behavior*	Low	3	Low	3
	Impacts of Tourism	Low-Medium	1	Medium	1
	Boat Strikes & Entanglement*	Low	1	Low	1

*Alone, these threats may not significantly contribute to the extinction risk of the species. But, in combination with other threats that, for example, decrease the abundance of the species (e.g., overutilization) or potentially affect important life history functions (e.g., climate change), these threats may exacerbate the impact of the other threats on the status of the species.

M. birostris

The most significant and certain threat to the giant manta ray is overutilization for commercial purposes. Giant manta rays are both targeted and caught as bycatch in a number of global fisheries throughout their range. Estimated take of giant manta rays, particularly in many portions of the Indo-Pacific, frequently exceeds numbers of observed individuals in those areas, and are accompanied by observed declines in sightings and landings of the species. Efforts to address overutilization of the species through regulatory measures appear inadequate, with evidence of targeted fishing of the species despite prohibitions (Indo-Pacific; Eastern Pacific) and only one regional measure to address bycatch issues, with uncertain effectiveness (Eastern Pacific). Additionally, given the migratory and pelagic behavior, national protections for the species are less likely to adequately protect the species from fisheries-related mortality. Giant manta rays are not confined by national boundaries and may, for example, lose certain protections as they conduct seasonal migrations or even as they move around to feed if they cross particular national jurisdictional boundaries (e.g., between the Maldives and Sri Lanka or India), move outside of established Marine Protected Areas, or enter into high seas. While the species recently has been added to CITES Appendix II (added in March 2013 with a delayed effectiveness of September 2014), which may curb targeted fishing as countries must ensure that manta ray products are legally obtained and trade is sustainable, the species is still likely to be caught as bycatch in the industrial fisheries and targeted by artisanal fisheries for domestic consumption.

Threats to *M. birostris* that were identified as potentially contributing to long-term risk of the species included (micro) plastic ingestion rates, increased parasitic loads as a result of climate change effects, and potential disruption of important life history functions as a result of increased tourism; however, due to the significant data gaps, the likelihood and impact of these threats on the status of the species is highly uncertain.

M. alfredi

Given their more inshore distribution and association with shallow coral and rocky reefs, *M. alfredi* does not appear to be as vulnerable to commercial and the larger-scale artisanal

fishing operations as *M. birostris*. These fisheries tend to operate in deeper and more pelagic waters, targeting migratory and commercially valuable species (like tunas, billfishes, and sharks), and, hence, have a higher likelihood of catching giant manta rays. In the available information, only two countries are reported to have targeted artisanal fisheries for *M. alfredi*: the Philippines (documented 4 fishing boats) and Mozambique. The species has been identified in bycatch from Indonesia, Papua New Guinea, and Kiribati, with subsequent observed declines in sightings, and potential local extirpations; however, the extent of fishing mortality on the species throughout its range is highly uncertain. In fact, many of the identified populations of *M. alfredi* throughout the western and central Pacific are currently protected by regulations and appear stable, indicating that these existing regulatory measures are adequate at protecting the species from declines due to fishing mortality. Within the Indian Ocean, national protections exist for the large population of *M. alfredi* off the Maldives, and while specific protections for *M. alfredi* have not been implemented in Western Australia, the species is not subject to directed fishing (or prevalent in bycatch) and is presently one of the largest identified populations.

Climate change was identified as a potential threat contributing to the long-term extinction risk of the species. Because *M. alfredi* are more commonly associated with coral reefs compared to giant manta rays, frequently aggregating within these habitats and showing a high degree of site-fidelity and residency to these areas, the impact of climate change on coral reefs was deemed a potential medium risk to the species. Although the species itself is not dependent on corals, which are most susceptible to the effects of climate change, the manta rays rely on the reef community structure, like the abundance of cleaner fish, to carry out important functions, such as removing parasite loads and dead tissue. Coral reef community structure is likely to be altered as a result of increasing events of coral bleaching through the foreseeable future; however, what this change will look like and its subsequent impact on the species is highly uncertain. Similarly, changes in zooplankton communities and distribution, including in and around coral reefs, are also likely to occur as a result of climate change, affecting the potential previous predictability of *M. alfredi* food resources. Reef manta rays may need to venture out farther to find available food or search for new productive areas; however, given that the species has been shown capable

of making long-distance foraging movements, the impact of this potential displacement or change in distribution of zooplankton may not be a significant contributor to the species' extinction risk.

Threats that were identified as potentially contributing to long-term risk of the species included (micro) plastic ingestion rates, increased parasitic loads as a result of climate change effects, and potential disruption of important life history functions or destruction of habitat as a result of increased tourism; however, due to the significant data gaps, the likelihood and impact of these threats on the status of the species is highly uncertain.

Overall Risk of Extinction

M. birostris

Given the species' extremely low reproductive output and overall productivity, it is inherently vulnerable to threats that would deplete its abundance, with a low likelihood of recovery. While there is considerable uncertainty regarding the species' current abundance throughout its range, the best available information indicates that the species has experienced population declines of potentially significant magnitude within areas of the Indo-Pacific and eastern Pacific portions of its range, primarily due to fisheries-related mortality. Yet, larger subpopulations of the species still exist, including off Mozambique, Ecuador, and potentially Thailand. However, as giant manta rays are a migratory species and continue to face fishing pressure, particularly from the industrial purse-seine fisheries and artisanal gillnet fisheries operating within the Indo-Pacific and eastern Pacific portions of its range, overutilization will continue to be a threat to these remaining *M. birostris* populations through the foreseeable future, placing them at a moderate risk of extinction.

While we assume that declining populations within the Indo-Pacific and eastern Pacific portions of its range will likely translate to overall declines in the species throughout its entire range, there is very little information on the abundance, spatial structure, or extent of fishery-related mortality of the species within the Atlantic portion of its range. As such, we cannot conclude that the species is at a moderate risk of extinction throughout its *entire* range. However, under the final Significant Portion of Its Range (SPR) policy, we must

consider whether the species may have a higher risk of extinction in a significant portion of its range (79 FR 37577; July 1, 2014).

Significant Portion of its Range Analysis

To identify only those portions that warrant further consideration under the SPR policy, we will determine whether there is substantial information indicating that (1) the portions may be significant and (2) the species may be at a higher risk of extinction within those portions. The SPR policy further explains that, depending on the particular facts of each situation, it may be more efficient to address the significance issue first, but in other cases it will make more sense to examine the status of the species in the potentially significant portions first. We have decided to go with the latter analysis.

As mentioned previously, the best available information indicates that the giant manta ray faces concentrated threats throughout the Indo-Pacific and eastern Pacific portion of its range. Estimated take of giant manta rays is frequently greater than the observed individuals in those areas, with observed declines in sightings and landings of the species of up to 95%. Efforts to address overutilization of the species through regulatory measures appear inadequate in this portion of its range, with evidence of targeted fishing of the species despite prohibitions and bycatch measures that may not significantly decrease fisheries-related mortality rates of the species. Based on the demographic risks and threats to the species in this portion, we found that the species has a moderate risk of extinction in this portion of its range.

Next, we must evaluate whether this portion is “significant.” As defined in the SPR Policy, a portion of a species’ range is “significant” “if the species is not currently endangered or threatened throughout its range, but the portion’s contribution to the viability of the species is so important that, without the members in that portion, the species would be in danger of extinction, or likely to become so in the foreseeable future, throughout all of its range” (79 FR 37578; July 1, 2014). Without the Indo-Pacific and eastern Pacific portion of the species’ range, the species would have to depend on only its members in the Atlantic for survival. While areas exhibiting source-sink dynamics, which could affect the survival of

the species, are not known, the largest subpopulations and records of individuals of the species come from the Indo-Pacific and eastern Pacific portion. The only data from the Atlantic on the abundance of the species are records of >70 individuals in the Flower Garden Banks Marine Sanctuary (Gulf of Mexico), >90 individuals off the east coast of Florida, and 60 manta rays from waters off Brazil. Given that the species is rarely identified in the fisheries data in the Atlantic, it may be assumed that populations within the Atlantic are small and sparsely distributed. These demographic risks, in conjunction with the species' inherent vulnerability to depletion, indicate that even low levels of mortality may portend drastic declines in the population. As such, without the Indo-Pacific and eastern Pacific portion, the minimal targeted fishing of the species by artisanal fishermen and bycatch mortality from the purse-seine, trawl, and longline fisheries in the Atlantic becomes a significant contributing factor to the extinction risk of the species, particularly as Chinese gill plate vendors have reported areas in South America (i.e., Brazil) as sources of their mobulid gill plates. Additionally, based on the AOO of the species within the Atlantic compared to those areas within the Indo-Pacific and eastern Pacific portion (**Figure 2**), suitable habitat may also be lacking, which would place the species at increased risk of extinction in the foreseeable future from threats that may adversely destroy or modify the current habitat, such as climate change. Based on the above findings, we conclude that the Indo-Pacific and eastern Pacific portion of the giant manta ray's range comprises a significant portion of the range of the species because this portion's contribution to the viability of *M. birostris* is so important that, without the members in this portion, the giant manta ray would likely become in danger of extinction within the foreseeable future, throughout all of its range.

Under the SPR policy, we conclude that the Indo-Pacific and eastern Pacific portion of the giant manta ray's range qualifies as a significant portion of the species' range, and based on the information above and further discussed in our demographic risks analysis and threats assessment, we conclude that *M. birostris* is at a **moderate risk of extinction** within this significant portion of its range.

Distinct Population Segment Analysis

In accordance with the SPR policy, if a species is determined to be threatened or endangered in a significant portion of its range, and the population in that significant portion is a valid distinct population segment (DPS), NMFS will list the DPS rather than the entire taxonomic species or subspecies. Because the Indo-Pacific and eastern Pacific represents a significant portion of the range of the species, and this portion is at a risk of extinction that is higher than “low,” we performed a DPS analysis on the population within this portion to see if it qualifies as a valid DPS.

The joint NMFS-U.S. Fish and Wildlife Service policy on identifying DPSs (61 FR 4722; February 7, 1996) identifies two criteria for DPS designations: (1) The population must be discrete in relation to the remainder of the taxon (species or subspecies) to which it belongs; and (2) the population must be “significant” (as that term is used in the context of the DPS policy, which is different from its usage under the SPR policy) to the remainder of the taxon to which it belongs.

In terms of discreteness, a population segment of a vertebrate species may be considered discrete if it satisfies either one of the following conditions: (1) “It is markedly separated from other populations of the same taxon as a consequence of physical, physiological, ecological, or behavioral factors. Quantitative measures of genetic or morphological discontinuity may provide evidence of this separation”; or (2) “it is delimited by international governmental boundaries within which differences in control of exploitation, management of habitat, conservation status, or regulatory mechanisms exist that are significant in light of section 4(a)(1)(D)” of the ESA (61 FR 4722; February 7, 1996).

As mentioned in the “Population Structure” section of this review, research on the genetics of the species, which may provide evidence of discreteness between populations, is ongoing. While there may be evidence of a potential *M. birostris* subspecies, or new manta species, found off the Yucatán coast in the Gulf of Mexico, Hinojosa-Alvarez et al. (2016) also showed that some of the Yucatán manta rays found in the area shared haplotypes with

M. birostris samples from the Indo-Pacific and eastern Pacific. Additionally, based on nuclear DNA, the Yucatán samples were consistent with the *M. birostris* samples from the Indo-Pacific and eastern Pacific portions of its range. As such, we do not find that the available data indicate genetic discreteness between *M. birostris* in the Atlantic and *M. birostris* in the Indo-Pacific and eastern Pacific. In terms of physical, physiological, morphological, ecological, behavioral, and regulatory factors, there is no evidence that the Indo-Pacific and eastern Pacific population of *M. birostris* is markedly separate from the population in the Atlantic. There is no evidence of differences in the morphology or physiology between the populations, nor any information to indicate changes in habitat use or behavior across ocean basins. Also, given that the species is highly migratory and pelagic, with no identified barriers to movement, these populations cannot be delimited by international governmental boundaries. As such, we find that the *M. birostris* population in the Indo-Pacific and eastern Pacific does not meet the discreteness criteria of the DPS policy, and, thus, is not a valid DPS.

M. alfredi

Overall, the species' life history characteristics increase its inherent vulnerability to depletion. Its tendency towards site fidelity and high residency rates suggests that there may be little gene flow between subpopulations, meaning that reestablishment after depletion is unlikely. Additionally, because these aggregations tend to be small, even light fishing may lead to population depletion. However, despite these inherent risks, the species does not appear to be subject to significant threats that are causing declines, or likely to cause declines, to the point where the species would be at risk of extinction. As mentioned in the threats analysis, targeted fishing of the species has only been observed in a select few locations, and its identification in bycatch is limited. The majority of the known *M. alfredi* subpopulations, particularly throughout the western and Central Pacific, while small, are protected from fishing mortality and appear stable. Some of the larger known *M. alfredi* subpopulations, such as off the Maldives (n=3,300-9,677) and Western Australia (n=1,200-1,500), are not subject to directed fishing, with Australia's overall population considered to be one of the world's healthiest. While climate change may alter aspects of the habitat and food resources of the species, the subsequent impact on the species is highly uncertain.

Thus, based on the above evaluation of demographic risks and threats to the species, we find that the reef manta ray is likely to be at a low overall risk of extinction.

SPR Analysis

As was done for the giant manta ray, we must conduct an SPR analysis to determine if the species is at a higher risk of extinction in a significant portion of its range. In applying the policy, we first examined where threats are concentrated to evaluate whether the species is at higher risk within those portions. Targeted fishing and subsequent declines in populations of *M. alfredi* are known from waters off Mozambique and the Philippines, and the species has also been identified in bycatch from Indonesia, Papua New Guinea, and Kiribati. However, with the exception of the southern Mozambique population, the extent of decline of the species throughout these other areas has not been quantified. But while the rate of decline is unknown, fishing pressure on the species continues in these portions of range and, combined with the species' demographic risks of isolated, small populations and extremely low productivity, these threats are likely placing these populations on a trajectory toward a higher risk of extinction.

The second question that needs to be addressed in the SPR analysis is whether these portions can be considered "significant." Without these portions, would the species be in danger of extinction, or likely to become so in the foreseeable future, throughout all of its range? We find that this is unlikely to be the case. Even if these populations were gone, the species would still exist as small, isolated populations throughout the Indo-Pacific. There is no evidence of source-sink dynamics between these portions and other areas, which could affect the survival of the species. In fact, the only indication of a potential source-sink dynamic was hypothesized for the *M. alfredi* population off Yaeyama, Japan, which Kashiwagi (2014) found is presently increasing, indicating no risk of loss to this population. In fact, many of the *M. alfredi* populations outside of the portions identified above, while small in size, are presently thought to be stable or increasing. Additionally, these populations, such as the largest identified *M. alfredi* population off the Maldives, benefit from national protections that prohibit the fishing, landing, or selling of the species. Because these populations occur nearshore, and the species exhibits high residency rates

and site-fidelity behavior, these protections will be adequate to prevent overutilization of the species through the foreseeable future. As such, even without the portions identified above, the species will unlikely be at a higher risk of extinction throughout all of its range now or in the foreseeable future.

Thus, under the SPR policy, we could not identify any portions of the species' range that meet both criteria (i.e., the portion is biologically significant *and* the species may be in danger of extinction in that portion, or likely to become so within the foreseeable future). Therefore, we find that our overall risk of extinction remains valid and conclude that *M. alfredi* is likely to be at a low risk of extinction throughout its range.

CONSERVATION EFFORTS

There are many conservation efforts presently ongoing to collect research on manta ray life history, ecology, and biology, and to raise awareness of threats to manta rays. Some of these efforts are spearheaded by non-profit organizations specifically dedicated to manta ray conservation, such as the Manta Trust (<http://www.mantatrust.org/>), the Marine Megafauna Foundation (<http://www.marinemegafauna.org/>), the Manta Pacific Research Foundation (<http://www.mantapacific.org/>) and MantaWatch (<http://mantawatch.com>). Others are driven by the countries whose economies largely depend on manta ray tourism (Erdmann 2014). The available research and citizen science data that have resulted from these conservation efforts have already been considered in the above analysis, and future research activities will continue to provide valuable information on these manta ray species.

The efforts by these organizations to educate the public, such as through awareness campaigns, could eventually lead to decreases in the demand for manta ray products. For example, Lawson et al. (2016), citing unpublished data, noted an 18-month awareness-raising campaign conducted in 2015 in Guangzhou, China that seemed to indicate a level of success in decreasing consumer demand of gill rakers, which, in turn, decreased the interest of traders to carry gill plates in the future. While more monitoring of trade and consumer behavior is required to evaluate the success of these efforts, it may indicate that

awareness-raising campaigns could be successful tools for influencing customer behavior and, as demand reduction is viewed as a potential avenue to indirectly reduce fishing pressure on manta rays, these campaigns may ultimately help decrease the main threat to the species (Lawson et al. 2016).

Additionally, awareness campaigns are also being used to educate the public on appropriate tourist behavior during manta ray dives, which can help decrease potential negative impacts of tourism activities on manta rays. As mentioned previously, best practice codes of conduct have been developed by a number of organizations and are increasingly being used by dive operators at a number of popular manta ray diving sites, including Kona, Hawaii, Western Australia, Mozambique, Bora Bora, and the Maldives, to promote the safe viewing of manta rays.

The International Union for Conservation of Nature (IUCN) Shark Specialist Group recently convened a workshop to develop a global devil and manta ray conservation strategy, which was released in 2016 (Lawson et al. 2016). This strategy is comprehensive in its goals to address the uncertainties that surround manta ray taxonomy, stock structure, biology and ecology and addresses the significant data gaps and potential threats to the species; however, the implementation plan and funding components of this strategy are unknown. As it stands, this strategy appears to be used presently as an informational document (see <http://www.iucnssg.org/conservation-strategies-devil-and-manta-rays.html>).

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APPENDIX

Legal Protections for Manta Rays (adapted from CITES 2013)

Location	Species	Legal Protection / Conservation Measure
International		
Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) Signatories	<i>Manta</i> spp.	CITES Appendix II , 2013
Convention on the Conservation of Migratory Species of Wild Animals (CMS) Signatories	<i>M. birostris</i> & <i>M. alfredi</i>	CMS Appendix I and II, 2011 & 2014, respectively
Regional		
The Inter-American Tropical Tuna Commission (IATTC) members	<i>Manta</i> spp.	Resolution C-15-04; Prohibition on retention, transshipment, storage, landing, sale of all devil and manta rays taken in large-scale fisheries. Must report mobulid catch data and ensure safe release; developing countries granted exception for small-scale and artisanal fisheries that catch them for domestic consumption, August 1, 2016.
Micronesia: Federated States of Micronesia, Guam, Mariana Islands, Marshall Islands, Palau	All ray species	Micronesia Regional Shark Sanctuary Declaration to prohibit possession, sale, distribution and trade of rays and ray parts from end 2012
National		
Australia	<i>Manta</i> spp.	Listed as migratory species under the Environment Protection and Biodiversity Conservation Act 1999
Brazil	<i>Manta</i> spp.	Instrução Normativa Interministerial no 2, de 13 de Março de 2013;

		Directed fishing and marketing of species, products and by-products of Mobulidae are prohibited. Additionally, gillnets and longlines are restricted between December and May, which is referred to as “manta ray season,” in order to avoid incidental captures of the species (Medeiros et al. 2015).
Ecuador	<i>M. birostris</i>	Ecuador Official Policy 093, 2010
European Union	<i>M. birostris</i>	Article 1 of COUNCIL REGULATION (EU) No 692/2012
Honduras	All elasmobranchs	Ban on fishing for elasmobranchs, 2010
Indonesia	<i>Manta spp.</i>	Minister of Marine Affairs and Fisheries 4/KEPMEN-KP/2014; established full protected status of <i>M. birostris</i> and <i>M. alfredi</i> in Indonesian waters (creating world’s largest manta ray sanctuary at around 6 million km ²).
Israel	All elasmobranchs	Protected in Israeli waters, 1980.
Maldives	<i>Manta spp.</i>	Exports of all ray products banned in 1995 and specifically the export of ray skins in 1996. Indirect forms of protection include prohibitions of most net fishing (including pelagic gillnets, trawling, and purse seining).
Mexico	All ray species	NOM-029-PESC-2006 Prohibits harvest and sale

New Zealand	<i>M. birostris</i>	Wildlife Act 1953 Schedule 7A (absolute protection), 2010
Peru	<i>M. birostris</i>	Ministerial Resolution 441-2015-PRODUCE; prohibits the landing, transport, capture, retention, processing, and/or sale of giant manta rays within marine Peruvian waters. Mantas that are caught as bycatch are to be immediately released alive and cannot be commercialized or used for human consumption, 2016.
Philippines	<i>M. birostris</i>	FAO 193 1998 Whale Shark and Manta Ray Ban
United Arab Emirates	<i>Manta spp.</i>	Manta rays fully protected in UAE waters, 2014
Yap (FSM)	<i>Manta spp.</i>	Manta Ray Sanctuary and Protection Act 2008; harming, killing, or destroying manta ray habitat is prohibited – covers an 8,243 square mile area around Yap, comprising 16 main islands and atolls and 145 islets.
State		
Florida, USA	Genus <i>Manta</i>	FL Admin Code 68B-44.008 – no harvest
Guam, USA Territory	All ray species	Article 1, Chapter 63 of Title 5, Guam Code Annotated, Sec. 63114.2
Commonwealth of the Northern Mariana Islands	All ray species	Public Law No. 15-124
Hawaii, USA	<i>Manta spp.</i>	HI Rev Stat Sec. 188-39.5
Raja Ampat Regency, Indonesia	<i>Manta spp.</i>	Shark and Ray Sanctuary Bupati Decree 2010; Regional Regulation 9/2012 (Regional law

		PERDA #9) prohibits the capture of manta rays in Raja Ampat waters.
West Manggarai, Indonesia	<i>Manta spp.</i>	No. DKPP/1309/VIII/2013; protection for mantas in the Komodo National Park
Marine Protected Areas (covering areas with observed manta presence)		
Cocos Island, Costa Rica	<i>Manta spp.</i>	Cocos Island National Park, 1978.
Guam	<i>Manta spp.</i>	Limited take MPA zone along northwest coast that covers around 57% of shore line where mean densities of manta rays for recent years (2008-2012) were highest (Martin et al. 2015).
Gulf of Mexico, USA	<i>Manta spp.</i>	Flower Garden Banks National Marine Sanctuary; Regulations prohibit killing, injuring, attracting, touching, or disturbing rays or whale sharks, except for incidental catch by conventional hook and line gear, 2012.
Eastern Australia	<i>Manta spp.</i>	Mantas occur in the Great Barrier Reef Marine Park, protected from fishing within “green zones.”
Maldives	<i>Manta spp.</i>	32 designated marine protected areas, of which 5 were specifically designated because of presence of mantas.
Pacific Remote Islands	<i>Manta spp.</i>	Pacific Remote Islands Marine National Monument, comprises approximately 370,000 square nm, encompassing 7 islands and atolls in Central Pacific Ocean.

		Commercial fishing is prohibited and no fishing is allowed within 12 nm of islands, 2009, 2014.
Philippines	<i>Manta</i> spp.	Tubbataha Reefs Natural Park was declared an MPA in 1988 and was expanded to include the Jessie Beazley Reef and a 10 nm buffer zone in 2010. Evidence of potential transient use by <i>M. alfredi</i> of the MPA (Aquino et al. 2015).
Revillagigedo Islands, Mexico	<i>Manta</i> spp.	Marine Protected Area, 1994, with 12-mile no-fishing zone surrounding each island.
Western Australia	<i>M. birostris</i>	16 Marine Parks designated along Western Australia's coast; includes Ningaloo Marine Park where manta rays are frequently observed and where <i>M. birostris</i> is protected from fishing and harassment. Protection for <i>Manta</i> spp. from recreational fishing only within "green zones" within state waters.
Yaeyama Islands, Japan	<i>Manta</i> spp.	Marine Protected Areas, 1998.